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Relative parental effort during incubation in rifleman (*Acanthisitta chloris*)

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Abstract The incubation system of rifleman was studied from 1980 to 1984 at Kowhai Bush, Kaikoura, New Zealand. Their nests are designed to maximise thermal insulation. So too is their behaviour, e.g., covering eggs and blocking the nest entrance with feathers. The outstanding feature of rifleman incubation is that males incubated for 48% and 45% of the time during first and second clutches, respectively, whereas the corresponding figures for females were both 33%. Hence females had about 60% more hours of daylight available for foraging than males. The difference in time spent incubating was because of longer incubation spells of males, rather than a higher frequency of visits to the nest. At night, females incubated while males roosted near the nest. The temperature inside the nest at night averaged 15°C and 12°C higher than that outside for first and second clutches, respectively. Rifleman have a highly co-operative parental care system during incubation which probably allows females to recoup condition after the expenditure of energy involved in laying a large clutch weight relative to the female's body weight.

Keywords Passerines; rifleman; Kowhai Bush; Kaikoura; incubation; parental effort; behaviour; co-operative parental care; thermal gradients

INTRODUCTION

Bi-parental care is considered the most widespread and primitive form of parental care in birds (e.g., Kendeigh 1952; Skutch 1957; Drent 1972). Amongst passerines, the female typically undertakes most, if not all, incubation (Skutch 1957). However, despite Skutch's generalisation, there are few studies that thoroughly measure relative parental effort and its variability. Hence few studies make any reliable generalisations about the species' relative parental effort during incubation.

Here I describe which parent usually performs most incubation in the rifleman (*Acanthisitta chloris*), a tiny (5–7 g) double-brooded hole-nesting Passerine. Also I offer an explanation for Skutch's (1957) generalisation not applying to this species. Parental care is quantified by attentiveness and the frequency of visits by day and night. In addition I describe the structure of the nest and the temperatures inside and outside the nest at night. The latter data are used to help determine if there was any advantage from thermal insulation to the bird occupying the nest at night. This study is part of a larger one of co-operative parental care in rifleman (see Sherley 1985, 1989, 1990), whose family (*Acanthisittidae*) is endemic to New Zealand.

METHODS

Rifleman were studied at Kowhai Bush near Kaikoura on the north-east coast of the South Island of New Zealand (42°23'S, 173°37'E). The native seral forest (85 hectares of predominantly kanuka, *Kunzea ericoides*) supported 27 to 33 pairs of rifleman, most of which were colour banded. Rifleman are sexually dimorphic and monogamous, which helped monitoring attentiveness at the nesting boxes. These boxes were built following the design used by Gray (1969), except that the entrance holes had a maximum width of 20 mm.

Second broods were those that followed the successful fledging of an earlier brood in the same season. First and second brood nests were removed

from boxes after fledging and weighed on Mettler electronic scales to the nearest 0.1 g.

The incubation period was divided into five 4-day intervals, counting the last egg laid as day 1, and the day before the first egg hatched as the last day of incubation. The available daylight hours (taken from sunrise to sunset, local time) over both incubation periods were divided into three equal intervals (subsequently referred to as "period of the day"). One hour intervals spent watching incubation were distributed as evenly as possible throughout the day. When a bird entered the nesting box it was assumed to be incubating. Numbers of visits to the nesting box perch and the frequency with which birds deposited feathers in the nest were also recorded.

Sampling protocol

The total time spent observing incubation was 218 h for first clutches and 153 h for second clutches, over three breeding seasons (1980/81, 81/82, 82/83). For any given period of the day during incubation (both clutches) there were: (i) between 6–19 occasions incubation was watched, (ii) 4–11 different pairs of birds sampled, and (iii) 2 or 3 different breeding seasons within which observations were made (Table 1).

Night time incubation was observed by noting the last bird entering the nest before darkness fell and then illuminating the box continuously with a 25 W, 12 V neon ultra-violet light. In addition, ad hoc spot checks were made on nests by briefly illuminating the nest bowl with a veterinary (5 mm diameter) anoscope. The sexually dimorphic head plumage of

rifleman allowed me to identify which parent was on the nest. Lights did not affect incubation behaviour since the neon light was switched on in complete darkness (usually an hour after the incubating bird had entered the nesting box) while the anoscope was usually unnoticed by the incubating bird.

Ambient air temperature was measured continuously on a thermograph in a standard New Zealand Meteorological Service instrument box located in a clearing within the study area.

Temperatures inside the nest were measured by placing a thermistor electrode in the bottom of the nest in the air space between the eggs. The thermistor was linked to a Grants thermograph which recorded temperature every 3 sec. The difference between nest-air temperature and ambient air temperature was calculated at 2 h intervals at least 2 h after sunset and 2 h before sunrise. These data were collected from two first clutch nests during September 1981 and two second clutch nests during November and December 1981. Measurements were taken evenly throughout incubation in one of each of the first and second clutch nests and similarly in the first half of incubation for the other two nests.

RESULTS

Nest structure

Rifleman built highly structured enclosed nests. The outer structure consisted of layers of tightly woven twigs and straw (about 35 mm thick) which became progressively finer towards the centre of the sphere (diameter about 35 mm). The nest cavity was lined with an outer layer of coarse feathers and an inner one of down feathers. The entrance tunnel was 11–30 mm wide and usually lead to the interior of the nest off centre from the hole in the nest box. This design appeared to optimise thermal insulation. Unlike first clutch nests, the second clutch nests were typically less structured and weighed significantly less ($x = 37.6$ g, $SD = 6.7$, $N = 46$; $x = 40.5$ g, $SD = 6.7$, $N = 124$, respectively; 1-tailed Mann Whitney U test $U = 3463.5$, $P < 0.02$). This difference may have been related to higher average ambient temperatures that occurred during second clutch incubation (late November, early December daytime mean air temperature was 12.9°C) compared with the first (September mean 9.4°C).

Incubation behaviour

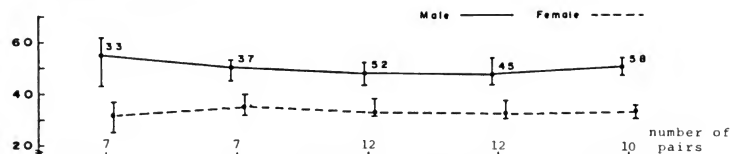
Both sexes had brood patches between the sterno-abdominal feather tracts. When not incubating,

Table 1 Details of observation protocol during first and second clutch incubation (1st, 2nd, 3rd = first, second, and third period of daytime observations, respectively).

	Incubation Intervals (days)											
	1–4			5–8			9–12			13–16		
	N	P	S	N	P	S	N	P	S	N	P	S
First clutch												
1st	13	5	3	13	7	3	18	10	3	11	7	3
2nd	9	5	3	13	5	3	15	11	3	21	11	3
3rd	11	5	2	11	6	2	19	9	3	13	10	3
Second clutch												
1st	8	4	2	9	5	3	6	4	2	10	6	3
2nd	10	5	2	10	6	2	13	8	3	11	6	2
3rd	7	4	2	9	5	3	14	7	3	12	5	2

N = number of hour-long observations; P = number of pairs observed; S = number of seasons over which observations were made.

A. FIRST CLUTCH



B. SECOND CLUTCH

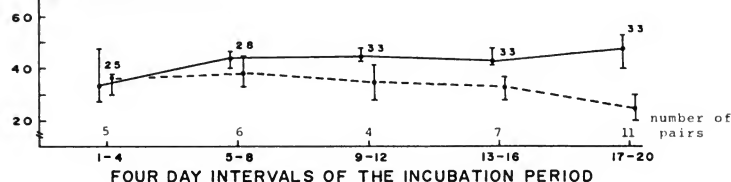


Fig. 1 (Proportions of time spent incubating (medians, 95% confidence intervals, and number of hour-long occasions spent observing). The number of pairs observed in each 4-day interval are shown. Confidence intervals calculated using method proposed by Snedecor & Cochran (1980)

males left eggs covered with down and the nest entrance blocked with feathers. Damp nest lining is continually replaced by both parents throughout incubation. Moisture was often brushed off a lining either on a perch before being returned by the parent. Before leaving the nest, a sitting bird usually waited for a specific call from its mate just outside the nest (Sherley 1985). For both clutches the length of the incubation period was 19.7 days (SD = 0.8, N = 10).

Work partition during incubation

The median attentiveness (proportion of time spent at the nest) of males and females during first clutch incubation was 48% and 33% (95% confidence intervals 47–52% and 32–35%, respectively, 225 one hour-observation periods). For second clutch incubation the corresponding figures for males and females were 45% and 33% (95% confidence intervals 42–47% and 30–35%, 152, one hour observation periods). Thus males spent about one and a half times longer incubating than females.

Although there was little variation in male attentiveness when incubating first clutches, their

median attentiveness in the first 8 days of incubating second clutches was 10–14% lower than that during the remainder of the incubation period (Fig. 1). The spells males spent sitting on the nest were usually significantly longer than those of females, except in the first half of the incubation period of second clutches when this pattern stopped (Table 2A, B). Thus the greater male attentiveness was generally a consequence of longer sitting spells (Table 2A) rather than a higher frequency of visits to the nest (Table 3).

The greater male attentiveness during first and second clutch incubation meant that females had about 2 h more daylight in which to forage.

Males and females were seen depositing a total of 80 and 42 feathers, respectively, into first clutch nests, and similarly 105 and 29 feathers into second clutch nests. A one-tailed Wilcoxon matched pairs sign rank test, comparing the frequency of feather delivery for parents each time a nest was watched, revealed males deposited significantly more feathers than females (standardised normal deviate $Z = -2.60$, $P = 0.01$; $Z = -4.12$, $P < 0.001$ for first and second clutches, respectively). Thirty-one checks were made on different nests between 1900 and 2200 h (N.Z.

Table 2A The periods parents spent on the nest, every time observations were made, have been compared using the Wilcoxon Matched Pairs Sign Rank Test (1-tailed). The test statistic and probabilities test the alternative hypothesis that males incubated for significantly longer periods than females. Key to columns: 1st, 2nd, and 3rd = first, second and third period of daytime observations, respectively.

		Incubation interval (days)				
1-4		5-8	9-12	13-16	17-20	
First clutch						
1st	12, <i>P</i> <.05*	7, <i>P</i> <.002*	11, <i>P</i> <.006*	11, <i>P</i> <.025*	3, <i>P</i> <.001*	
2nd	14, <i>P</i> >.05	12, <i>P</i> <.008*	16, <i>P</i> <.005*	20, <i>P</i> <.003*	34, <i>P</i> <.002*	
3rd	1, <i>P</i> <.002*	18, <i>P</i> >.05	24, <i>P</i> <.003*	11, <i>P</i> <.005*	6, <i>P</i> <.001*	
Second clutch						
1st	8, <i>P</i> >.05	18, <i>P</i> >.05	2, <i>P</i> >.05	8, <i>P</i> <.05*	7, <i>P</i> <.005*	
2nd	22, <i>P</i> >.05	13, <i>P</i> >.05	7, <i>P</i> <.002*	13, <i>P</i> <.05*	11, <i>P</i> <.005*	
3rd	7, <i>P</i> >.05	15, <i>P</i> >.05	20, <i>P</i> <.003*	13, <i>P</i> <.02*	0, <i>P</i> <.02*	

Note: Where an asterisk occurs (i.e., where $P < 0.05$), males spent significantly longer on the nest than females.

Table 2B The average proportions of time spent incubating by parents throughout both incubation periods. Key to columns: 1st, 2nd, and 3rd = first, second and third period of daytime observations, respectively. M = male, F = female.

		Incubation interval (days)									
		1-4		5-8		9-12		13-16		17-20	
		M	F	M	F	M	F	M	F	M	F
First clutch											
1st	0.49	0.29	0.50	0.35	0.50	0.34	0.47	0.39	0.51	0.33	
2nd	0.47	0.39	0.48	0.35	0.49	0.32	0.40	0.41	0.50	0.32	
3rd	0.50	0.26	0.47	0.36	0.48	0.35	0.47	0.36	0.48	0.32	
Second clutch											
1st	0.38	0.31	0.39	0.47	0.49	0.43	0.47	0.36	0.49	0.28	
2nd	0.36	0.35	0.40	0.37	0.45	0.28	0.42	0.30	0.41	0.28	
3rd	0.21	0.35	0.42	0.38	0.43	0.33	0.43	0.35	0.51	0.20	

Table 3 Hourly visits to nests to incubate by rifleman parents during the incubation period.

		Incubation interval (days)									
Days	1-4		5-8		9-12		13-16		17-20		
First clutch											
x	M	F	M	F	M	F	M	F	M	F	
SD	3	5	2	2	3	2	2	2	3	2	
N	1	4	0.7	0.9	2	0.7	1	1	0.7	0.7	
Z	33		37		52		45		58		
	0.31(NS)		0.77(NS)		2.41(P=0.001)		1.21(NS)		2.44(P=0.001)		
Second clutch											
x	3	5	3	2	3	2	5	8	3	5	
SD	1	3	1	1	1	1	3	6	1	0.4	
N	25		28		33		33		33		
Z	1.34(NS)		1.08(NS)		2.27(P=0.04)		0.77(NS)		0.54(NS)		

M = male, F = female, x = mean, SD = standard deviation, N = sample size, Z = standardised normal deviate statistic for 2-tailed Wilcoxon matched pairs sign rank test, NS = not significant.

Standard Time) over two seasons, and each time the female was sitting. Feathers blocked the entrance on four occasions. Watching nests from sunset to dark on four occasions (including one nest on three occasions) revealed that females incubated throughout the night. The difference between the average nest-air temperature and the ambient air temperature (both nests) for first clutches was 15°C ($N = 4$, $N = 96$ measurements), and for second clutches 12°C ($SD = 4$, $N = 71$).

DISCUSSION

During incubation, rifleman are faced with heating a relatively huge egg mass that is on average 84% of male body weight in first clutches (Sherley 1989) and 105% of male body weight (Sherley 1985). This is achieved through co-operative bi-parental care where the male spends more time on the nest.

Nest structure and parental behaviour conserved energy by increasing thermal insulation and reducing cooling rate of eggs. Efficient thermal insulation was achieved by using progressively finer layers of tightly-woven materials in nest construction, and by partitioning the nest entrance tunnel off centre from nest box entrance, thereby reducing draughts and loss of warm air. Furthermore, egg cooling rates were reduced by the efficient swapping of incubation duties by the parents; a sitting bird usually waited for a specific call from its mate whereupon the latter immediately entered the nest. The importance of efficient nest attentiveness has been illustrated in a study of house wren (*Troglodytes aedon*) eggs, which took 1.6 times longer to heat up than cool down (Kendeigh 1963).

Covering eggs with feathers when leaving the nest must reduce the cooling rate of eggs. Similarly, drying dry feathers to the nest, drying out the existing lining by teasing feathers on a perch, and blocking the entrance tunnel with feathers at night to reduce draughts, would have had the same effect.

Night-time incubation by females gave them a thermal insulation advantage over males which roosted outside in the relative cold. Walsberg & King (1978a) showed that energy expenditure of incubating mountain white-crowned sparrows (*Monticola leucophrys oriantha*) was 15% less than those roosting outside the nest. This difference may be greater for rifleman than for the sparrows because the nests of rifleman are fully enclosed (wing hole nesters) rather than cup shaped.

The drop in male attentiveness at the nest for the last 8 days of second clutch incubation (Fig. 1)

probably occurred because the male undertook most of the feeding of first brood fledglings, which only became independent part way through second clutch incubation (Sherley 1985, 1990). Since feeding young is energetically more expensive than incubating (Ricklefs 1974), the males' behaviour was consistent with the hypothesis that rifleman adopt a highly co-operative system of parental care.

The smaller contribution of females than males to feeding second brood fledglings (Sherley 1990), and their apparent unwillingness to increase attentiveness early in second clutch incubation, when the males' attentiveness has declined, may reflect their need to recoup energy after the demands of laying the second clutch. A second clutch amounts to about 72% of the female's body weight (Sherley 1989). Unlike when laying first clutches, females are unaided by courtship feeding before and during laying second clutches (Sherley 1989). The demands of egg-laying have been shown to be responsible for a drop in intra-muscular protein in the Quelea bird (*Quelea quelea*), which is recouped during incubation (Jones & Ward 1976). In rifleman, 2 h of extra foraging time is available to the female during incubation compared to the male, and this probably allows her to regain condition after laying.

In daytime, incubation probably incurs a net loss of energy relative to foraging, especially as the latter should, logically, return a net gain. Despite the controversy over whether or not incubation costs energy (see Walsberg 1977, 1983; Walsberg & King 1978b), there is evidence that incubation does incur a net loss of energy (i.e., productive energy; Kendeigh 1963). Although this might be true of the rifleman female incubating at night, the male probably loses still more energy roosting outside. I propose that rifleman do not conform to Skutch's (1957) generalisation that females undertake most incubation for passerines because by co-operating in parental care they may increase productivity. Co-operation is achieved by structured work partitioning which effectively allows them to care for the fledglings of the first brood (see Sherley 1990) while incubating the second clutch.

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Evidence for the displacement of an endemic New Zealand spider, *Latrodectus katipo* Powell by the South African species *Steatoda capensis* Hann (Araneae: Theridiidae)

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Abstract The competitive interactions between *Latrodectus katipo* and *Steatoda capensis* were studied under the hypothesis that *L. katipo* is being displaced from its natural habitat by competition from *S. capensis*. Use of trophic and spatial resources were studied. High overlap for both resources was found. Data on reproductive potential revealed that *S. capensis* has a significantly higher reproductive output. Laboratory predation experiments indicated *L. katipo* adults are not inferior to *S. capensis*. Evidence suggesting displacement following *L. katipo* population crashes was obtained. Differences in reproductive potential and seasonal reproduction are proposed as the mechanism underlying the displacement.

Keywords *Latrodectus katipo*; *Steatoda capensis*; competition; reproductive potential; displacement

INTRODUCTION

Latrodectus katipo Powell 1870 is a theridiid spider endemic to New Zealand and restricted to coastal regions, mainly at sandy beaches (Forster & Forster 1973).

A decline in the abundance of *L. katipo* in some lower North Island regions in the last 10–15 years has been noted by various sources. Dr G. W. Gibbs (Victoria University of Wellington – pers. comm.) has reported that *L. katipo* was common up to the late

1970s in the Cook Strait coast between Pencarrow and Fitzroy Bay, but was not found in this area during a search in 1983. He has also reported that *L. katipo* was present at "Wharekauhau" beach (Palliser Bay) in the late 1970s. I have made two extensive searches of this beach in consecutive years (1983–1984) and failed to reveal one *L. katipo*. In each of these situations a species of *Steatoda* was abundant.

R. Ordish (National Museum, Wellington—pers. comm.) has reported that there was a dense population of *L. katipo* at Hokio beach in 1970 but that by 1983 the species had become very scarce, with a species of *Steatoda* previously not seen at this beach outnumbering *L. katipo* by at least 50:1.

D. Laing (119 Creswick Tce, Wellington—pers. comm.) in searches conducted in 1984 and 1985 from Paekakariki to Waikanae found no *L. katipo*. He did, however, find limited numbers of *L. katipo* along the coast between Himatangi and Tangimoana. A species of *Steatoda* was abundant in both these areas. Searches I conducted in 1989 at Baring Head, Waikanae, Paraparaumu, Hokio beach, and Pukepuke Lagoon beach had similar results, i.e., either there were no *L. katipo* present (as with the first two sites named) or there were very few *L. katipo* but abundant specimens of one *Steatoda* species.

I have identified the *Steatoda* species which is now so common along the Wellington coast as a South African species described by O. P. Cambridge (1903) as *Teutana lepida*, and have given this species the new name of *Steatoda capensis* for reasons outlined elsewhere (Hann 1990). Identification was made initially using the description given by Cambridge (1903), and was confirmed by examining both male and female specimens on loan from the South African Museum. Cambridge described specimens from Cape Town but apparently *S. capensis* is fairly widely distributed throughout South Africa and is frequently recorded in and around houses (Dr Dippenaar-Schoeman, Plant Protection Research Institute, Pretoria—pers. comm.). I have observed *S. capensis* along the coast and associated with houses in Nelson, Blenheim, Wellington, and New Plymouth, with a wide range of web sites

including the base of rose bushes and under corrugated iron, wooden planks, and concrete bricks. Examination of a *Steatoda* collection belonging to the Plant Protection Centre (Ministry of Agriculture and Fisheries, Auckland) revealed *S. capensis* to be a common species in the Auckland region. It is also widespread on the coast of the East Cape.

The recent disappearance of *L. katipo* from areas where it used to be common and the abundance of *S. capensis* in these areas, suggests the hypothesis that *L. katipo* is competitively inferior to *S. capensis* and as a consequence is being displaced from its natural habitat.

The existence of interspecific competition in spiders has been questioned (Wise 1984) as a result of a number of researchers finding no significant interspecific competition in their studies of spider communities (Wise 1981; Horton & Wise 1983; Riechert & Cady 1983). Alternatively, Brown (1981) concluded there was inferential evidence of interspecific competition among orb weavers and Spiller (1984) found interspecific competition between spiders was significant and appeared to play an important role in structuring their community. Nyffeler et al. (1986), in a study similar to the present one, concluded that competition was occurring between *Steatoda bipunctata* (Linnaeus) a European immigrant into North America, and *S. borealis* (Hentz) a native North American species, leading to the displacement of the latter. The two species are the same size, show a high level of micro-habitat and diel activity overlap, and both select the same prey species at the same rate (Nyffeler et al. 1986). Although Nyffeler et al. (1986) felt that displacement was occurring they were unable to identify the mechanism by which it was operating. *S. borealis* (the displaced species) actually appeared to be more likely to win an agonistic interaction with *S. bipunctata* in screen-cage laboratory experiments and *S. bipunctata* appeared to have no advantages in its reproductive potential or seasonal life history (Nyffeler et al. 1986).

Spiller (1984) suggests predators or abiotic factors of mortality may have reduced spider abundance in some of the above studies, thus reducing competition. This suggestion is supported by Enders' explanation of the coexistence of two species of orb weavers (Enders 1974) and by Gertsch & Riecherts' explanation of the coexistence of congeneric species in the absence of niche partitioning (Gertsch & Riechert 1976). Other researchers (Uetz 1977; Turner & Polis 1979; Kessler et al. 1984) reported temporal, spatial, or trophic specialisation as means of reducing

niche overlap between spider species. As pointed out by Colwell & Futuyma (1971), niche overlap values can be used as evidence for or against interspecific competition. Thus, the low overlap values of these researchers may be evidence of no competition or could equally well be the result of intense competition which lead to segregation along a resource dimension. However, niche overlap values are valuable as indicators of the degree to which the species examined jointly use a resource.

The following study examines the assumptions that interspecific competition does occur in spiders, and that the distribution of one species may be limited by the presence of another species through competition (Krebs 1978). The study involved: (1) assessing species distribution patterns in relation to habitat and to each other; (2) assessing spatial and trophic niche overlaps; (3) a small population manipulation experiment; (4) assessing reproductive potential; and (5) conducting laboratory predation experiments.

STUDY SITE

The study site is an area of sand dune beach (173°02'E 41°06'S lat) in Motueka, (Nelson, New Zealand), in the form of a flat spit bounded by the sea and tidal mudflats. In 1984 it was clearly divided into: a densely vegetated zone (habitat A) made up mainly of tree lupin (*Lupinus arboreus*) with marram grass (*Ammophila arenaria*) on the outer edges of the lupin and large patches of iceplant (*Carpobrotus edulis*) among the lupin; and a sparsely vegetated zone (habitat B) made up of clumps of marram grass and isolated tree lupin plants. Habitat A extended approximately 274 m along the study area, with habitat B comprising the last 140 m. In subsequent years, the lupin and marram spread throughout habitat B and by 1987 there was no clear separation of the habitats.

METHODS

Logs occupied by *L. katipo* or *S. capensis* were located by a systematic search of the study area. All logs and areas of congregated small driftwood in the study area were searched as were areas of iceplant and marram grass. For each occupied site, i.e., isolated log or clump of marram, the number of spider occupants and their species was recorded. To determine species habitat distribution pattern, the spider's location was recorded as either habitat A or habitat B. χ^2 analysis was used to determine whether

Fig. 1 Changing abundance of species over time (Habitat A).

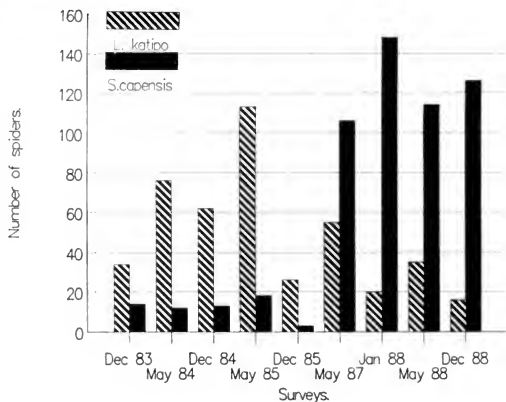
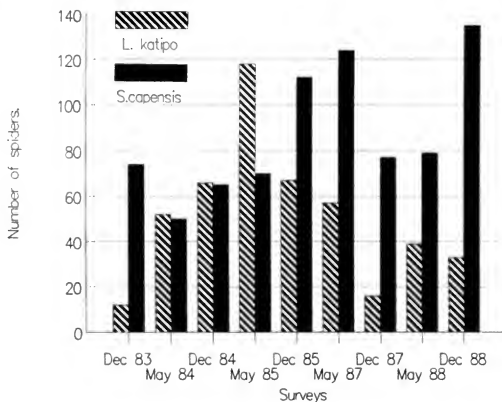


Fig. 2 Changing abundance of species over time (Habitat B).



the two species were distributed independently of habitat. A coefficient of association V was calculated for each species, where V varies from -1 (negative association) to $+1$ (positive association) and is 0 when there is no association (Krebs 1978).

Two methods were used to investigate distribution of *L. katipo* in relation to *S. capensis*. The first involved recording the presence/absence of each species at each site. Data were analysed using Sorensen's test which gives a value from $0-1$, 0 indicating no association and 1 indicating perfect association, i.e., where one species occurs the other will always occur. The second method involved recording the species of the nearest neighbour for each spider. χ^2 analysis was used to indicate whether the number of times one species was the nearest neighbour of the other was different from that expected assuming random distribution. A measure of segregation S (Pielou 1961) was calculated, where S varies from -1 (negative segregation, i.e., the nearest neighbour is always the other species), to $+1$ (positive segregation i.e., the nearest neighbour is always a conspecific), and 0 if the two species are mixed.

Data were gathered on the spiders' use of spatial and trophic resources. Web presence in marram was recorded, whereas size (surface area) of inhabited logs was recorded and logs grouped into four size categories: $<1200 \text{ cm}^2$, $1200-2400 \text{ cm}^2$, $2400-3600 \text{ cm}^2$, and $>3600 \text{ cm}^2$. These data were analysed to see if species had preferred web sites and if they overlapped in this resource component.

Nine surveys were conducted spanning 5 years. The month and year of each survey are given in Fig. 1 and 2. In survey 1, food use was determined by collection of prey from webs of a randomly selected sample of spiders (35% total population). All webs were collected and examined for the presence of food items and rebuilt webs were collected at the end of each of the following 2 weeks. In survey 3, old webs were collected from all sites still occupied (some spiders had left their webs since the initial observation), this being 83% of *L. katipo* webs and 75% of *S. capensis* webs. All rebuilt webs were collected 3 weeks later as part of survey 3. Availability of prey in each habitat was estimated in 1984 by pitfall trapping, which also provided intact specimens for identification of prey taken from webs. A χ^2 test for heterogeneity was conducted on pitfall-trap data to establish whether different prey species were available in the two habitats. χ^2 tests were also carried out where possible to test for differences between the two species in their use of prey within habitats.

Niche overlap values were calculated from data on the spiders' use of four resource dimensions, namely habitat used, food species habitat A, food species habitat B, and web site preference. The equation used to calculate unidimensional niche overlap was

$$\alpha_{jk} = \frac{\sum p_{ij} \cdot p_{ik}}{\sqrt{\sum p_{ij}^2 \cdot \sum p_{ik}^2}}$$

where P_{ij} and P_{ik} represent the proportions of the i th resource used by the j and k th species (Pianka 1974).

At the end of survey 1, a population manipulation experiment was begun. This involved releasing 12 *L. katipo* among the resident *S. capensis* in habitat B and 24 *S. capensis* among the resident *L. katipo* in habitat A. The introduced spiders were monitored for 3 weeks after release. All spiders were introduced into an area where conspecifics were scarce (i.e., <3 conspecifics within 10 m of the release site) so marking was not considered necessary.

In surveys 6-9 the number of egg sacs per spider and the number of immatures and males were recorded.

Laboratory predation experiments were conducted in 1984. These involved placing one *L. katipo* and one *S. capensis* female into a wooden enclosure measuring 200 mm long \times 150 mm wide \times 15 mm deep, with a 10 mm lip under which the spiders could live, a removable median partition, and a glass top. Spiders were weighed before the experiment using a Mettler H10 to ± 0.0005 g with paired spiders matched on weight equality. At the start of a trial the two spiders were set into the enclosure one either side of the partition. After webs were established the partition was removed. A trial was judged complete either when one spider was killed or died naturally.

RESULTS

Distribution

Distribution of spiders between the two habitats is shown in Fig. 1 and 2.

Table 1 Habitat overlap values.

Survey								
1	2	3	4	5	6	7	8	9
0.49	0.74	0.85	0.87	0.94	1.0	0.98	0.97	0.95

The salient features are: (1) the distribution of *L. katipo* between habitat A and B has changed from being predominantly habitat A at Survey 1 (73.9%) to an even distribution by surveys 3–4 and 6–9. By survey 5, *L. katipo* numbers in habitat A decreased dramatically due to severe storm damage; (2) *S. capensis* distribution has changed from predominantly habitat B (90–97%) in surveys 1–5, to a more even distribution in surveys 6–9; (3) *L. katipo* numbers increase during summer with a maximum in late autumn (May), followed by a decrease over winter; whereas (4) in general, *S. capensis* numbers are greatest in mid-summer (December) and decrease slightly through the autumn; and (5) *L. katipo* dominated all surveys except one up to 1985, whereas *S. capensis* dominated at all surveys after May 1987.

Habitat association

The habitat overlap values indicate a high degree of overlap for all surveys except survey 1 (Table 1). These results reflect the fact that *L. katipo* spread into habitat B after survey 1 and *S. capensis* spread into habitat A after survey 5.

The χ^2 analysis of habitat association indicates that for surveys 1–5 *L. katipo* occurred more often in habitat A and less often in habitat B than expected if one assumed a random distribution across habitats (Table 2). The coefficients of association all indicate negative association with habitat B.

Conversely, in surveys 1–5, *S. capensis* occurred more often in habitat B and less often in habitat A than expected and the *V* values indicate positive association with habitat B (Table 2). However, the situation changes in surveys 6–9 when both species occur as often as expected in each habitat given

random distribution. All *V* values for both species for surveys 6–9 indicate no association with either habitat, i.e., *V* values all approach zero. This change is mainly because before survey 6 *S. capensis* was found almost exclusively in habitat B, but in surveys 6–9 it is also found throughout habitat A. *L. katipo* distribution had already spread over the two habitats by survey 3.

Species association at web sites

All Sorensen values for species association at web sites were low (Table 3) indicating *L. katipo* and *S. capensis* rarely occur at the same site.

The two species occur together at only 5.80% of all sites observed over the nine surveys. This result may be because of the spiders' tendency to occur alone (*L. katipo* in particular—Table 4) or it may reflect interspecies avoidance. As Table 4 shows, *L. katipo* normally occurs alone whereas *S. capensis* occurs mainly alone or with one or more conspecific, i.e., least often with *L. katipo*.

Analysis of nearest neighbour data revealed *L. katipo* and *S. capensis* were associated in a significantly non-random manner (Table 5), with the measures of segregation indicating positive segregation, i.e., the nearest neighbour is usually a member of the same species.

These results support the idea that the two species avoid each other.

Web site

Analysis of web site data revealed that both species used the two smaller classes of log most often. Use by *L. katipo* varied from 91.3% of spiders at survey

Table 2 Results of χ^2 analysis of habitat association data. Coefficients are *V* values and indicate the degree of association of the species with habitat B.

Survey	<i>L. katipo</i>			<i>S. capensis</i>		
	Coeff. assoc.	χ^2	<i>P</i>	Coeff. assoc.	χ^2	<i>P</i>
1	-0.56	33.58	<0.00001	+0.57	35.35	<0.00001
2	-0.36	21.42	0.00001	+0.40	26.91	<0.00001
3	-0.30	15.64	0.00008	+0.41	29.24	<0.00001
4	-0.22	11.33	0.0008	+0.27	16.47	0.00005
5	-0.29	11.40	0.0008	+0.37	19.20	0.00001
6	-0.04	0.51	0.48 NS	+0.06	0.93	0.33 NS
7	+0.07	1.32	0.25 NS	-0.05	0.04	0.84 NS
8	+0.15	5.06	0.024 NS	-0.10	2.29	0.13 NS
9	+0.10	2.89	0.089 NS	-0.12	3.6	0.058 NS

Table 3 Results of analysis of species association at sites.

	Survey								
	1	2	3	4	5	6	7	8	9
Sorensen's value	0.10	0.07	0.13	0.23	0.18	0.14	0.03	0.10	0.008

N.B. Values of 0 indicate no association i.e., the two species never occur together. Values of 1 indicate complete association i.e., the two species always occur together

Table 4 Percentages of each species population occurring alone, with conspecifics or with other species at a site (i.e., isolated log or clump of marram).

Survey	<i>L. katipo</i>			<i>S. capensis</i>		
	Alone	+Consp.	+ <i>S. capensis</i>	Alone	+Consp.	+ <i>L. katipo</i>
1	89.1	0	10.9	54.5	37.5	8.0
2	84.4	6.2	9.4	61.3	21.0	17.7
3	83.6	6.3	10.1	56.4	21.8	21.8
4	55.0	27.7	17.3	40.9	12.5	46.6
5	78.5	6.4	15.1	22.6	57.4	20.0
6	62.5	17.0	20.5	64.4	25.6	10.0
7	91.7	0	8.3	69.7	28.1	2.2
8	63.5	18.9	17.6	72.5	19.7	7.8
9	98.0	0	2.0	61.3	38.3	0.4

Table 5 Results of nearest neighbour analysis. *S* values are measures of segregation and vary from -1 (the NN is always the other species) to +1 (the NN is always a conspecific).

	Survey							
	1	3	4	5	6	7	8	9
χ^2	38.6	12.7	11.8	30.8	27.2	5.2	14.0	6.4
Measure of segregation	+0.55	+0.25	+0.19	+0.38	+0.28	+0.10	+0.23	+0.14

Note: All χ^2 values significant at $P < 0.001$, except for survey 7 and 9 where P is between 0.025 and 0.01.

Table 6 Web site overlap values.

	Survey								
	1	2	3	4	5	6	7	8	9
	0.77	-	0.76	0.96	-	0.97	0.98	0.99	0.99

Table 7 Percentage of each species using marram or small logs in surveys 4 and 6.

	Web site	<i>L. katipo</i>	<i>S. capensis</i>
Survey 4	Small logs*	54.5%	67.0%
	Marram	42.0%	31.8%
Survey 6	Small logs*	54.6%	60.9%
	Marram	36.6%	24.8%

*Small logs indicates $< 1200 \text{ cm}^2$ and $1200\text{--}2400 \text{ cm}^2$ categories.

54.5% at survey 4, whereas *S. capensis* use varied from 53.8% at survey 1 to 85.5% at survey 7. This accounts for the high overlap values gained for web use (Table 6).

Use of marram grass for web sites was normally low, i.e., less than 15% of sites used by both species surveys 1–3 and 7–9, but during surveys 4 and 6 when the total spider population was over 300 the

percentage of spiders using marram increased notably (Table 7). Smith (1971) found 89% of 187 *L. katipo* in marram grass at South Brighton beach in Christchurch, and the other 11% mainly in Pingao (*Desmoschoenus spiralis*). However, as Smith (1971) points out, *L. katipo* at this beach did not have the opportunity to inhabit driftwood which is removed by inhabitants of New Brighton.

Table 8 Pit-fall trap data from 155 pit-fall traps and actual prey data for surveys 1 and 3.

Prey Order/species:	Potential prey (Pit-fall trap data)		Actual prey			
	Habitat A	B	<i>L. katipo</i>		<i>S. capensis</i>	
			A	B	A	B
ISOPODA						
<i>Talorchestia quoyana</i>	79.98	74.75	36.11	70.26	33.33	72.76
COLEOPTERA						
<i>Cecyropa lucunda</i>	5.53	4.32	43.01	16.92	33.33	9.70
<i>Mimopeus elongatus</i>	NA	NA	8.63	0.51	11.76	NA
<i>Ceratognathus irroratus</i>	NA	NA	1.26	2.22	NA	3.36
<i>Costelytra zealandica</i>	NA	NA	0.94	1.54	1.96	1.49
<i>Pericoptus truncatus</i>	NA	NA	0.47	0.34	NA	NA
<i>P. truncatus</i> larvae	<.01	0.10	0.94	0.34	NA	NA
<i>Xyloteles griseus</i>	1.00	0.10	0.63	NA	NA	NA
<i>Thelyphassa diaphana</i>	1.28	1.08	0.31	0.85	1.96	4.85
<i>Cafius quadri-impressus</i>	NA	NA	0.16	0.17	1.96	NA
<i>Lagrioda browni</i>	1.06	3.53	0.16	1.71	NA	NA
<i>Laemostenus complanatus</i>	0.44	NA	0.16	NA	NA	NA
<i>Conoderus exsul</i>	NA	NA	NA	NA	7.84	1.49
<i>Prionopus reticularis</i>	NA	NA	NA	0.17	NA	NA
DERMAPTERA						
<i>Forficula</i> sp.	1.40	0.10	3.92	0.17	3.92	NA
<i>Anisolabis littorea</i>	NA	NA	0.16	NA	NA	NA
HYMENOPTERA						
<i>Apis mellifera</i>	NA	NA	0.78	0.34	1.96	1.12
<i>Vespula germanica</i>	NA	NA	NA	NA	NA	0.37
HEMIPTERA						
<i>Hahnia australis</i>	NA	NA	1.10	NA	NA	NA
LEPIDOPTERA						
<i>Uresipheta polygonalis</i> #	0.73	0.98	0.47	NA	NA	NA
<i>Agrotis ipsilon aneituma</i>	0.28	0.69	0.16	0.34	NA	1.87
<i>A. i. aneituma</i> larvae	NA	NA	0.31	2.91	NA	0.37
ARANEAE						
<i>Dolomedes minor</i>	0.39	NA	NA	0.51	1.96	NA
<i>Dysdera crocata</i>	<.01	NA	0.16	NA	NA	0.37
Amaurobid unidentified	NA	NA	0.16	NA	NA	NA
Lycosid unidentified	0.44	1.47	NA	0.17	NA	NA
Theridiid unidentified	NA	NA	NA	0.51	NA	2.23
Non-prey species	8.28	12.87				
ACTUAL NUMBERS	1789	1018	708	608	86	342

#*U. polygonalis* larvae

NA = Not Applicable, meaning never observed.

Note: data from the first "old webs" collected at survey 1 are not included in the table as this early data was not kept separate by habitat. This data is given in Hann (1984).

This increased use of marram during times of high population suggests a limited number of suitable log sites. During survey 9 there was an abundance of small driftwood and the number of spiders using marram grass was again low, even though the spider population was over 300.

Prey

All pitfall trap items are listed in Table 8 along with actual prey for surveys 1 and 3. χ^2 analysis of pitfall trap data for items which contributed greater than 1.0% of either species diet revealed a significant difference in prey available in the two habitats ($\chi^2 = 41.7, P < 0.001$). The main contributors to the difference were *Lagriodabrowni* and *Forficula* sp. Web analysis supports this conclusion and also shows that *Cecyropa lucunda* and *Mimopeus elongatus* were much more common prey items in habitat A than habitat B. This difference makes separate analysis of web contents necessary for the two habitats.

Analysis of web contents revealed these spiders to be euryphagous predators. From the 2048 prey items collected overall there were 30 taxonomic groups. The major prey items were *Talorchestia quoyana* (51.72% survey 1, 55.32% survey 3) and *C. lucunda* (23.15% survey 1, 27.0% survey 3). A detailed breakdown of web contents for survey 1 is given in Hann (1984).

For habitat A the two species use of five prey species (*T. quoyana*, *C. lucunda*, *Forficula* sp., *M. elongatus*, and *Ceratognathus irroratus*) was χ^2 tested using data from survey 3 and "rebuilt web" data from survey 1. These five species combined represent 93% and 86% of the diet of *L. katipo* and *S. capensis*, respectively, in habitat A. The results indicate prey use is significantly different from expected ($\chi^2 = 12.5, 0.005 < P < 0.01$) reflecting that *L. katipo* eat proportionally more *C. lucunda* and less *T. quoyana* than expected, whereas *S. capensis* does the reverse.

For habitat B the two species use of six prey species (*T. quoyana*, *C. lucunda*, *C. irroratus*, *Agrotis ipsilon aeneituna* larvae, *Thelyphassa diaphana*, and *Costelytra zealandica*) were χ^2 tested. These six prey species combined represent 94% and 89% of the diet of *L. katipo* and *S. capensis*, respectively, in habitat B. The result indicates prey use is significantly different from expected ($\chi^2 = 23.4, P < 0.001$) reflecting the fact that *L. katipo* eat proportionally more *C. lucunda* and less *T. diaphana* than expected, whereas *S. capensis* does the reverse.

Overlap values indicate a high degree of prey-use overlap.

Population manipulation

The introduction of 24 *S. capensis* to habitat A had no apparent effect. None of the released spiders could be found 3 weeks after release and *S. capensis* numbers at the next survey were not higher as might have been expected. The 12 *L. katipo* released in habitat B were all located after release, 10 of them occupying small logs. At the end of 3 weeks nine were still present, one having been eaten by another *L. katipo* and two disappearing after a spring tide flooded their logs. As the *L. katipo* numbers increased dramatically in habitat B by survey 2 it seems likely that most of the remaining *L. katipo* introductions survived and reproduced.

Predation experiments

Of 28 trials which yielded results, *L. katipo* killed *S. capensis* in 19 trials whereas *S. capensis* killed *L. katipo* in 9 trials. These results indicate that an adult female *L. katipo* is more likely to win an agonistic interaction with an adult female *S. capensis* ($z = 1.89, P = 0.0588$). There was no significant difference between the weight of the surviving spiders (mean = 0.1017 g, = 0.0284 g) and those that were killed (mean = 0.1044 g, SD = 0.0345 g; $t = 0.31, P > 0.10$).

Reproductive potential

The ability to produce offspring may provide an advantage to one species or the other (Nyffeler et al. 1986). Although Nyffeler et al. (1986) found that *S. bipunctata* and *S. borealis* have a very similar life history and sexual behaviour, the present study indicates two major and important differences in reproductive biology between *L. katipo* and *S. capensis*. Firstly *S. capensis* egg sacs contain, on average, a little less than three times the number of eggs that *L. katipo* sacs contain (Table 10). However, as *S. capensis* spiderlings emerge from the sac as first instars, their mortality rate may be much higher than that of *L. katipo* spiderlings, which emerge as larger second instars.

Table 9 Overlap values for prey use.

	Habitat A	Habitat B
Survey 1	0.68	0.93
Survey 3	0.92	0.96

Secondly, *S. capensis* reproductive output during winter is much higher than that of *L. katipo* (Table 1). During winter the mean number of egg sacs per spider is significantly greater for *S. capensis* and the proportion of the *S. capensis* population with egg sacs is much higher. Although the mean number of egg sacs per spider is greater for *L. katipo* in the summer surveys this point is overshadowed at surveys 1 and 9 by the fact that for each reproductive *L. katipo* there are at least five reproductive *S. capensis*, thus total output is in favour of *S. capensis*. The mean number of egg sacs per spider has increased significantly for *S. capensis* from survey 3 to survey 9 ($P = 3.28, P = 0.001$).

S. capensis immatures and males were more abundant than for *L. katipo* at all times of year (Table 1).

The majority of the *S. capensis* immatures observed at these surveys occurred at web sites occupied by *S. capensis* adults (i.e., 60% immatures with adults at survey 6, 87.9% at survey 7, 95% at survey 8, and 96.1% at survey 9). The small number of *L. katipo* immatures makes identifying a similar trend difficult.

DISCUSSION

What caused the initial division of species over habitats? The preference of *L. katipo* for habitat A may be linked to its preference for *C. lucunda* which occurs more commonly in the dense lupin area. Spiders are known to respond to such variations in habitat quality, e.g., Riechert & Tracy (1975) found choice of web site in *Agelenopsis aperta* was influenced by temperature and the presence/absence of ground depressions. The absence of *S. capensis* in habitat A cannot be attributed to choice of habitat B as preferred habitat because by survey 6 *S. capensis* has become abundant in habitat A with no change in the characteristics of this habitat. It is

possible that the dominance of *L. katipo* in habitat A at surveys 2–4 prevented expansion of *S. capensis* into this area.

Why did the distributions change?

There are two possible causes for the increase of *L. katipo* in habitat B from survey 1 to survey 4: (1) the 12 introduced *L. katipo* from the population manipulation experiment gave *L. katipo* a more stable breeding population or (2) the increase of *L. katipo* was a consequence of the spread of the dense lupin into and right through habitat B. *L. katipo* also increased in habitat A over this period but from Fig. 1 it can be seen that this is part of a seasonal fluctuation pattern.

The distribution of *S. capensis* remained stable until survey 6 which was conducted 17 months after habitat A was destroyed by a combination of severe storms and high tides. These storms in late 1985 caused lupin to die off, flattened the marram grass and swept away driftwood. The *L. katipo* population declined from 113 in May 1985 to 26 in December 1985. While a seasonal decline over this period is expected the decline was magnified by the destruction of habitat. This conclusion is supported by the fact that in habitat B *L. katipo* only declined from 118 to 67. Seventeen months later, in May 1987, *L. katipo* numbers have increased but to nowhere near the level of May 1985, whereas *S. capensis* numbers had exploded from 18 (May 1985) to 106 (May 1987). This population explosion following the reduction of *L. katipo* numbers supports the idea that *S. capensis* was previously limited to habitat B by the dominance of *L. katipo* in habitat A. In the months after the storms of late 1985 there would have been many vacant potential web sites into which *S. capensis* could migrate either from habitat B or more likely from the fields behind habitat A, without encountering interference from *L. katipo*. It seems more likely that migration of *S. capensis* into such vacant sites lead to the establishment of this species in habitat A by May 1987 rather than direct displacement of *L. katipo* adults from web sites by *S. capensis* adults. The latter is unlikely for a number of reasons: (1) an established species has a competitive advantage over an immigrating species (Riechert & Cady 1985); (2) *L. katipo* consumes other spiders so the probability of a web takeover by another spider species is probably low (Riechert & Cady 1983); and (3) laboratory trials have shown that an adult *L. katipo* is more likely to kill an adult *S. capensis* than be killed in a conflict at a web site (Hann 1984).

Table 10 Eggsac data from field collected sacs.

	Number of sacs	Mean No. of eggs/sac	Standard deviation	Range
<i>S. capensis</i>	37	183.6	53.9	92–309
<i>L. katipo</i>	23	68.3	21.0	34–115

Note: As the sacs were field collected it is not known whether each sac represents the 1st, 2nd, or 3rd egg sac produced by the spider for that summer. The mean is thus mean for all egg sacs.

Are limited resources causing interspecific competition?

By survey 6 the two species show total overlap in habitat use and the question arises of whether they can coexist in this distribution or will interspecific competition lead to the displacement of one species.

The two species show a high degree of overlap in all resource dimensions examined. The overlap values for prey use were particularly high. The proportion of each species diet which appeared as exclusive to that species was very small, and given further data would probably disappear altogether. However, there is no evidence that prey is a limited resource so even though the diet of the two species overlap almost completely this should not be used as an indication of interspecific competition (Riechert & Cady 1983). Also the fact that the two species show significant differences in the proportions in which they consume certain prey species would suggest that coexistence is possible in this resource dimension. High overlap values were obtained for preferred web site. Both species appeared to prefer to build webs under the smaller-sized logs. One difference which did separate the two species was that *S. capensis* would occupy logs located among damp depressions which *L. katipo* appeared to avoid. This last observation supports Forster's hypothesis (1984) that *Latrodectus* species prefer habitats of low relative humidity. However, even with *S. capensis* using these damp sites there is a finite and relatively small number of suitable logs or suitable marram sites. Webs were only located in older dense

marram clumps and most of the marram was young and open. Smith's (1971) observations also indicate *L. katipo* prefer medium to dense marram. Thus although prey may not be limiting it seems likely that availability of suitable log sites will be a limiting factor. Riechert & Cady (1983) found space afforded suitable characteristics for web construction to be limiting to spiders in their study. That log sites are limited is supported by the increase of use of marram grass during high total population numbers. Interspecific competition for web sites therefore seems likely. In interactions at web sites between *L. katipo* and *S. capensis* in laboratory trials, the most common result was the predation of *S. capensis* by *L. katipo* (Hann 1984). This was so for spiders showing no significant size (weight) difference; however, where *L. katipo* is likely to be disadvantaged by competition for web sites is in the establishment of immature spiders at web sites. Results show that *L. katipo* normally occurs alone whereas *S. capensis* is much more likely to tolerate the presence of conspecifics, with instances of four to six adult *S. capensis* occurring at one site, plus immatures. *S. capensis* and *L. katipo* adults, however, consistently showed no association at sites. In terms of immatures seeking web sites this suggests that *L. katipo* immatures would be rejected by both established *L. katipo* and *S. capensis* web owners, whereas *S. capensis* immatures are less likely to be rejected by established *S. capensis* web owners, resulting in a higher than usual mortality rate for *L. katipo* immatures. This theory is supported by immature numbers recorded during surveys 6-1.

Table 11 Species egg sac production in summer (surveys 3, 7, and 9) and winter (surveys 6 and 8) showing the number of spiders with sacs, total number of egg sacs, the percentage of the population with egg sacs, and the mean number of egg sacs per spider.

Survey		Number spiders with sacs	Total sacs	% popn	Mean no. of sacs/spider	SD	z value	Signif. level
3	<i>L. katipo</i>	89	155	69.5	1.21	1.12	5.37	<0.0001
	<i>S. capensis</i>	30	40	38.4	0.51	0.75		
7	<i>L. katipo</i>	23	49	63.9	1.36	1.30	2.45	0.014
	<i>S. capensis</i>	157	184	70.1	0.82	0.62		
9	<i>L. katipo</i>	39	90	79.6	1.84	1.37	4.22	<0.0001
	<i>S. capensis</i>	194	257	74.3	0.99	0.74		
6	<i>L. katipo</i>	2	2	1.8	0.02	0.13	7.7	<0.0001
	<i>S. capensis</i>	61	64	26.5	0.28	0.47		
8	<i>L. katipo</i>	5	5	6.8	0.07	0.25	3.13	0.0018
	<i>S. capensis</i>	37	38	19.2	0.20	0.41		

Note: the mean number of egg sacs per spider was calculated from all observations i.e., including observations of zero.

which greatly favours *S. capensis* (Table 12). Spiller (1984) has shown that interspecific exploitative competition for a resource can become a limiting factor for a spider species. As well as being rejected from suitable web sites it is likely that many immature *L. katipo* are predated upon during their attempts to occupy web sites already occupied by *S. capensis* which have matured during the winter/spring months. Spiller (1984) found such interspecific interference significant between spiders which showed seasonal differences in size.

Is displacement of *L. katipo* occurring?

Since the destruction of habitat A in late 1985 and the consequent decimation of the *L. katipo* population, *S. capensis* appears to have undergone competitive release in this habitat. After conducting removal experiments Riechert & Cady (1983) sought three kinds of evidence for competitive release: (1) changes in densities of juveniles and adult spiders; (2) changes in level of egg production; and (3) shifts in microhabitat use. The first criterion is clearly satisfied for adults and juvenile densities have also increased (Table 12).

The second criterion also appears to be satisfied. The average number of egg sacs per spider for *S. capensis* has increased significantly from survey 3 to survey 7, as has the proportion of the *S. capensis* population producing egg sacs (Table 11). Comparing the same period the egg sac production for *L. katipo* has not changed significantly (Table 11).

As no food data was collected at survey 6 or survey 8 it is not possible to say whether *S. capensis* has changed its use in prey species, for example in increasing its consumption of *C. lucunda*. There has been no apparent change in web site use by *S. capensis* since survey 5. Thus, only two of the three forms of evidence for competitive release have been satisfied.

Competitive release of *S. capensis* following natural or accidental human-related reduction of the *L. katipo* population is one explanation for the colonisation of *L. katipo* habitat by *S. capensis*. The alternative is that *S. capensis* is a relatively recent

introduction into New Zealand and it is only now reaching the *L. katipo* habitat where it is displacing *L. katipo* by direct competition. Although it seems likely that *S. capensis* is a recent immigrant, I do not believe it is displacing *L. katipo* by direct competition. Evidence suggests the former explanation is more likely.

After natural destruction of a segment of its habitat, *L. katipo* could recolonise in one of two ways, either by lateral migration of spiders from adjacent undamaged habitat, or by replacement with new spiders from summer reproduction. Given low *L. katipo* numbers either method is likely to be a slow process. Colonisation of the damaged habitat by *S. capensis* could be much more rapid, either by large-scale immigration of spiders from adjacent inland habitat where *S. capensis* occur with no competition from *L. katipo*, or by new spiders from reproduction by *S. capensis* already in the area. *S. capensis* continue to reproduce year round and produce significantly more eggs per sac than *L. katipo*, two features which would aid it in rapid colonisation of vacant habitat. If *S. capensis* can recolonise more quickly than *L. katipo* then it would gain the competitive advantage of being the established species and *L. katipo* immatures would find it difficult to locate free web sites. Given this situation it is likely that *L. katipo* would be permanently displaced from this area.

CONCLUSION

The displacement of *L. katipo* by *S. capensis* at the study site was triggered by a dramatic decline in the *L. katipo* population size after storm damage to the *L. katipo* habitat. Displacement at other sites, such as Hokio Beach (Wellington) may also have been triggered by natural acts or by human interference with the habitat. Nyffeler et al. (1986) found that the permanent displacement of *S. borealis* by *S. bipunctata* was restricted to those parts of the habitat range most influenced by human activity. L. Forster (100 Norfolk St, Dunedin—pers. comm.) has suggested that the lack of *L. katipo* along the Otaki-Wanganui coast may be related to the substantial modification of the sand dunes by construction of parking lots, barbeque areas, etc. and a consequent change in vegetation. The destruction or modification of habitat may lead to the habitat becoming totally unsuitable for the narrow-niched *L. katipo*, in which instance the effect of *S. capensis* would be irrelevant. However, if the habitat is not rendered entirely unsuitable for *L. katipo* then the population should

Table 12 Comparison of numbers of immatures and males seen for each species at surveys 6–9.

Survey	6	7	8	9	6	7	8	9
	Number of immatures				Number of males			
<i>L. katipo</i>	2	9	4	5	4	4	1	1
<i>S. capensis</i>	85	33	126	26	40	6	39	15

slowly recover in the absence of *S. capensis*. In my view the presence of *S. capensis* can have a significant effect and lead to permanent displacement of *L. katipo* because *S. capensis* can colonise the newly vacant web sites faster than *L. katipo* can recolonise them. *S. capensis* can colonise a vacant habitat quickly because: (1) *S. capensis* immigrants are available from inland which is not true for *L. katipo*; (2) the reproductive rate of *S. capensis* is higher than that of *L. katipo*; and (3) *S. capensis* reproduce year round whereas *L. katipo* produce very few egg sacs in the winter months.

There is no evidence to suggest that adult *L. katipo* spiders are competitively inferior to adult *S. capensis* spiders; on the contrary, *L. katipo* adults appear to be superior in instances of direct agonistic interactions. Similarly, in limited laboratory trials Nyffeler et al. (1986) found *S. borealis* to be the consistent winner in antagonistic interactions against *S. bipunctata*, even though in the wild it is being displaced by *S. bipunctata*. Where *S. capensis* is likely to gain an advantage once it has become established is in competition for web sites between homeless immature *L. katipo* and web-occupying mature *S. capensis*. In this situation, the immature *L. katipo* would be inferior and be chased from the web site or predated. So, by its ability to rapidly colonise vacant habitat and become the dominant established species, *S. capensis* displaces *L. katipo* from its previous habitat.

As *S. capensis* is an introduced species this phenomenon may be relatively new, but combined with increasing human interference along coastal areas it is likely that *L. katipo* will continue to decline in areas in which it was once common, and finally be totally displaced by *S. capensis*.

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Changes in the diversity of New Zealand forest birds

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Abstract Shannon diversity indices for several fossil assemblages of New Zealand birds are compared with estimates for living communities today. As expected, bird species diversity was higher in the pre-human environment, but it was also greater than that predicted from studies of living communities. Previous estimates of the number of terrestrial bird species in the pre-human avifauna are too low, and many of these were incorrectly interpreted as being open-country species. The pre-human fauna was deficient in open-country birds. A prediction based on biogeographic (species-area) theory that this deficiency in open-country species was filled by half the species of moa (*Dinornithiformes*) is not supported by palaeoecological evidence. The major fall in bird species diversity in New Zealand is linked to the type of forest removed in Polynesian times, as well as the area.

Keywords bird species diversity; Shannon Index; forest birds; extinction; habitat

INTRODUCTION

Compared with other land masses of equal size closer to continental land masses, New Zealand has relatively few species of terrestrial birds (Slud 1976). The present terrestrial avifauna consists of species which have survived the environmental changes of the past 1000 years, and about 25 introduced species.

The indigenous terrestrial birds are mainly forest species, and several of these are rare or restricted to large forest areas and inshore or offshore islands. Most of the introduced species avoid dense, wet native forest, but some, such as the chaffinch (*Fringilla coelebs*), song thrush (*Turdus philomelos*), and European blackbird (*T. merula*), penetrate deep into native forest stands and are now part of the forest ecosystem. Various studies (e.g., Kikkawa 1966), have examined the relative abundance of forest species in the present fauna, and McLay (1974) estimated the diversity of forest birds within different forest types and suggested some consequences of further forest loss and modification.

Although there is general awareness that the present indigenous fauna is the remnant of a much larger fauna, there have been few attempts to quantify the changes in the avifauna, apart from listing the birds which have been extirpated on each island. McLay (1974) predicted the diversity of forest birds in pre-European New Zealand, but did not extend this to pre-human times, or have data to test his prediction.

Flux (1989) calculated the expected number of species in the original fauna, according to island biogeographic theory. From the expected number of species on a landmass of New Zealand's size (Slud 1976), and assuming an equilibrium between open-country and forest species, he suggested that several species of moa (*Dinornithiformes*) occupied open (i.e., non forest) habitats. There has been considerable controversy over moa habitat and the total number of species (e.g., Anderson 1990; Atkinson & Greenwood 1989; Caughley 1977; Duff 1956). Flux (1989) argued from species-area relationships for the whole avifauna that there were "a total of 8–12 species [of moas], evenly distributed between forest and open-country". This would mean that four to six species of moa were primarily open-country birds. The discussion depends on the definition of forest bird: Flux (1989) defined a forest bird as one which "relies on" forest, whereas I prefer the broader definition of birds which have stable, long-term, forest populations.

Flux's interpretation of total number of species depends in part on the definition of a land bird, and he followed Slud (1976) in excluding all rails and waterfowl. The applicability of this definition to New Zealand and other island ecosystems is evaluated here.

Recent publications on subfossil bone deposits in New Zealand include enough data on the relative abundance of species to allow a preliminary test of McLay's (1974) prediction of forest bird diversity, extended to pre-human times, to be made. The recent expansion in knowledge of the temporal and geographic distribution of extinct species (e.g., Worthy 1987, 1989a), data on distribution and composition of vegetation in pre-human and pre-European times (McGlone 1980, 1983; Nicholls 1980), and more secure systematic treatment of the moas (Cracraft 1976; Millener 1982; Worthy 1987, 1988, 1989b; Anderson 1990) also enable Flux's predictions to be tested. This paper presents the results of an analysis of faunas from four sites, ranging in age from Otiran glacial at c. 20 000 yr B.P., to the midden deposits of an early Polynesian community (600–900 yr B.P.).

METHODS

Diversity

I calculated Shannon diversity indices ($H' = -\sum p_i \log_e p_i$; $H_{max} = \log_e S$, and $J = H'/H_{max}$ where p_i is the proportion of the total number of individuals belonging to the i th species and S is number of species) for four fossil avifaunas, using published data on minimum numbers of individuals recorded. Three of the four sites: Poukawa, Washpool midden, and F1 cave are in the North Island; the fourth, Honeycomb Hill Cave System, is in the South Island. The deposits are mostly Holocene in age, but Layer 3 of the Graveyard deposit at Honeycomb Hill caves is Pleistocene (Worthy & Mildenhall 1989). The sites were chosen because of the completeness of published information on numbers of individuals, and because present information suggests that they were forested during the period(s) of deposition. Species lists for the sites are given in Table 1.

For the Honeycomb Hill cave (Oparara) and Poukawa sites, diversity indices were calculated for each stratigraphically distinct layer, or for the stratigraphic subdivision of the site used by each author (Poukawa). Graveyard Layers 1 and 2 from Oparara (Worthy & Mildenhall 1989) were pooled; indices were calculated for the pooled fauna and for

the Eagle's Roost (Oparara) fauna, and for Graveyard Layers 1 and 2 (c. 14 000–10 000 yr B.P. plus surface Holocene material) and Eagle's Roost faunas (16 000 yr B.P.–present) pooled. Worthy & Mildenhall (1989) indicated that the faunas were both accumulating in the Holocene, and they are so close geographically that they were probably sampling the same life assemblage. However, different depositional regimes and greater representation of the late Holocene in Eagle's Roost have resulted in different species representations at these sites.

The calculated values for fossil faunas were compared with McLay's (1974) predicted value of H' for the pre-European avifauna (Fig. 1) by plotting them on his fig. 1. To examine the relationship between H' values for fossil and living assemblages, I plotted H' for native forest species from McLay (1974) against $\log_{10} S$, and calculated the regression line. Regressions for the pooled fossil assemblages, and for all assemblages, were also calculated (Fig. 2b). The lines were then replotted on normal axes (Fig. 2c, based on McLay's (1974) fig. 1).

The evenness (J) value for each fossil assemblage was compared with those from modern sites reported by McLay (his fig. 2). The Shannon index depends on two variables: the number of species, and their relative representation, in the sample. Evenness is a measure of the departure of the sample from the limiting situation where all species are equally represented, and was used here only to see if the fossil assemblages differed greatly from the living samples in the proportions of individual species represented.

Values of H' and H_{max} for fossil assemblages were plotted on fig. 4 of McLay (1974) to enable a comparison with living New Zealand forest bird assemblages, and with the predicted diversity before European settlement.

Species-area relationships and New Zealand forest birds

Only the South Island fauna was analysed. Four lists of forest bird species breeding on the South Island were prepared: 1, using Flux's (1989) lists (working back from number of species reported) for A.D. 1840; 2, Flux's list plus other birds present in A.D. 1840 which, although they can live in open habitats, also live in forest; 3, list 2, plus extinct species, which by analogy with living relatives elsewhere, inhabited forest; 4, list 3, plus moas.

The numbers of species in each of these lists were plotted on fig. 1 of Flux (1989). Flux's point for species number for the South Island in A.D. 1840

table 1 Minimum numbers of individuals for forest bird species in fossil sites used in the analysis. Data for Waitomo from Worthy (1984); Poukawa from Horn (1983); Washpool from Leach (1979); and Oparara from Worthy & Mildenhall (1989).

Species	Site									
	Waitomo			Washpool			Oparara			
	F1b	F1c Layer 2/4	F1c 8 r	Poukawa Layer 1 2 3	midden	Graveyard Layer 1/2	3	Eagle's Roost	Eagle's Roost + Gyd 1/2	
<i>nomalopteryx didiformis</i>	7	7	1	3		2			2	
<i>legapteryx didinus</i>						4	73	3	7	
<i>uryapteryx curtus</i>	1									
<i>uryapteryx geranoides</i>	1			1	2					
<i>achyornis mappini</i>	1	3	1	5						
<i>achyornis elephantopus</i>							4			
<i>achyornis australis</i>							30			
<i>tinornis struthoides</i>	2	1	1					1	1	
<i>tinornis novaeseelandiae</i>		1	1	1			1			
<i>tinornis giganteus</i>	1									
<i>pteryx australis</i>	1	6	3	2			1}	3}	3}	
<i>pteryx haasti</i>							}	}	}	
<i>pteryx oweni</i>	2	8	1					1	1	
<i>pteryx sp.</i>	1	8								
<i>myiarchus finschi</i>		4	3	1	3	26	17			
<i>nemiornis septentrionalis</i>			2	3						
<i>nemiornis calcitrans</i>								1	1	
<i>callirallus philippensis</i>				1	1		1			
<i>callirallus australis</i>	7	51	6	2	43	133	76	3		
<i>capellirallus karamu</i>	1	1	1	8	41	22	3	5	9	14
<i>callinula hodgeorum</i>					4	32	15	2	1	1
<i>lorzana sp.</i>					2	5	3			3
<i>ulica chathamensis</i>						8	4			
<i>porphyrio mantelli</i>	3	22	6	1	2	44	26		4	
<i>ptornis otidiformis</i>	2	2	2	1	1			2		
<i>oenocorypha aucklandica</i>	1	2	1		3	2		1	4	5
<i>lapagornis moorei</i>								5	2	2
<i>ircus eylesi</i>	2			2	13	12		1	1	1
<i>alco novaeseelandiae</i>				2	9	4		2		
<i>linox novaeseelandiae</i>					2					
<i>celoglaux albifacies</i>	1			2	2			4	4	4
<i>lestor notabilis</i>								34	17	1
<i>lestor meridionalis</i>		1		6	39	18	4			35
<i>trigops habroptilus</i>	11	21	5	1	4	34	29	1		
<i>yanoramphus novaeseelandiae</i>				6	9	6		2)	1)	8)
<i>yanoramphus auriceps</i>				1	2	1	95))))
<i>temipha novaeseelandiae</i>			3	8	28	16	12			
<i>legotheles novaeseelandiae</i>								4	1	4
<i>calcyon sancta</i>										5
<i>canthisitta chloris</i>										
<i>enicus longipes</i>		1	1						21	21
<i>enicus gilviventris</i>									12	12
<i>raversia lyalli</i>									35	36
<i>achyplichas jagmi</i>	1	1							14	19
<i>achyplichas yaldwyni</i>										
<i>Vren n. gen. n. sp.</i>									36	37
<i>etroica australis</i>									1	1
<i>etroica macrocephala</i>									49	52
<i>rosthemadera novaeseelandiae</i>				7	5	1	87		10	10
									2	2

(continued)

Table 1 (continued)

Species	Waitomo			Poukawa			Site	Oparara			Eagle's	
	F1b	F1c Layer		1	2	3	Washpool midden	Graveyard Layer	3	Eagle's Roost	Eagle's Roost + Gyd 1/2	
		2/4	8 r									
<i>Anthornis melanura</i>							1			2	2	
<i>Rhipidura fuliginosa</i>							1			2	2	
<i>Mohoua novaeseelandiae</i>										5	5	
<i>Mohoua ochrocephala</i>										6	6	
<i>Mohoua albigilla</i>		1										
<i>Gerygone igata</i>										1	1	
<i>Callaeas cinerea</i>	3	6	7	1	8	19	13	2	6	5	55	61
<i>Philesturnus carunculatus</i>		1			2	8	2	2	1		9	10
<i>Heteralocha acutirostris</i>								1				
<i>Turnagra capensis</i>								3				
<i>Corvus moriorum</i>					9	3			1	5	1	4

Note: Horn (1983) noted that much of the moa material from Poukawa was unidentifiable, but included *Pachyornis mappini* and species of *Euryapteryx*.

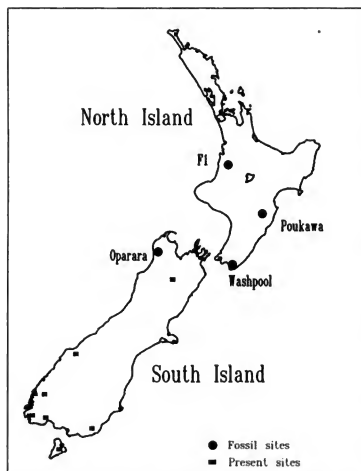


Fig. 1 Map of New Zealand showing location of major fossil sites referred to in this study, and general location of virgin forest sites used in McLay (1974).

was replotted using an estimate of South Island forest cover at European settlement based on McGlone (1989). This was done because Flux appears to have plotted the point at an estimate of forest area based on both islands, which grossly underrepresents the amount of forest lost from the South Island by 1840. The areas used here were 90% forest cover in pre-human period, reduced by 50% during Polynesian period, which gave a maximum forest cover at A.D. 1840 of 45% of land area. Most of that remaining in A.D. 1840 was high altitude beech forest or wet podocarp hardwood associations to the west of the main mountain ranges.

The curve (based on Arrhenius's power function) for species number against percent forest cover was replotted through the revised point (above). A curve using the species number from list 2 above at A.D. 1840 was also calculated, to pass through a corresponding point, also at 45% forest cover.

Species numbers from the four lists were plotted on fig. 2 of Flux (1989) for comparison with Flux's (1989) estimates of total number of land bird species, and number of "forest" and "open-country" species (Fig. 4).

RESULTS

Diversity

The values of H' calculated for the fossil assemblages were of the same order as those reported by McLay (1974) for present day assemblages including

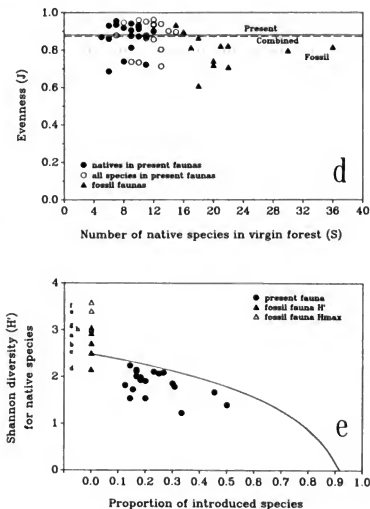
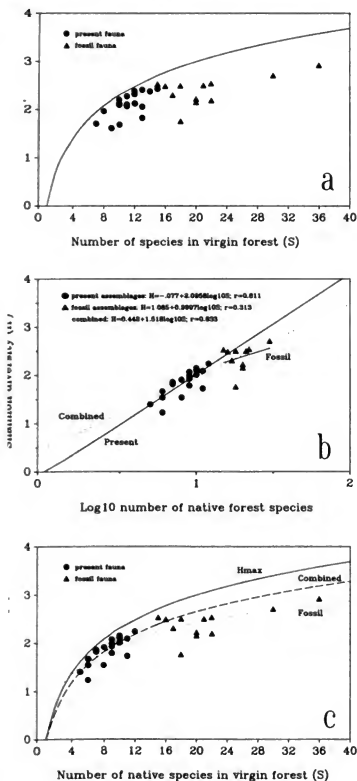


Fig. 2 (a-e) a Shannon diversity indices (H') for extant and fossil bird assemblages in virgin New Zealand forest. Data for extant assemblages from McLay (1974). The curve is H_{max} . b Shannon diversity against log₁₀ of the number of native forest bird species in extant and fossil assemblages. Least squares regression lines and regression equations are shown for extant (=present) assemblages (long solid line), fossil assemblages (short solid line), and both assemblages combined (dotted line). c Regression lines and data points from Fig. 2b, plotted on normal axes. Solid line is H_{max} , dotted line is regression for fossil assemblages, and dashed line is regression for combined samples. d Evenness (J) of extant and fossil New Zealand forest bird assemblages. Solid line indicates mean value for extant assemblages, dotted line indicates mean for fossil assemblages, and dashed line the mean for all assemblages. e Prediction of diversity indices for pre-European bird assemblages. Points for present faunas from McLay (1974); curve is H_{max} for 12 native species in the present fauna, for increasing proportions of introduced species. Predicted value for pre-European is intercept of curve with y-axis (McLay 1974). Filled triangles are H' values for: a, Eagle's Roost + Graveyard L1+L2; b, Eagle's Roost; c, Poukawa L3; d, Graveyard L3. Open triangles are H_{max} values for: e, Eagle's Roost; f, Eagle's Roost + Graveyard L1+L2; g, Poukawa L3; h, Graveyard L3.

introduced species (Fig. 2a). Maximum diversity as obtained for the most "complete" fauna (graveyard Layers 1 and 2 plus Eagle's Roost). The values of H' for present day native bird assemblages are highly correlated with the log of species number, $H' = 0.077 + 2.0958 \log_{10} S$, $r = 0.811$; Fig. 2b).

H' values for fossil assemblages showed greater scatter, but the combined data sets also gave a highly significant correlation (Fig. 2b). H' values for all fossil assemblages were generally higher than for

present native bird faunas, but they decreased less rapidly with increasing H_{max} (Fig. 2c; solid line) than expected from the least squares line calculated from present faunas (Fig. 2c: broken line). The least squares regression for the fossil and present native faunas combined is shown by the dotted line in Fig. 2c.

Evenness (J) values for present and fossil faunas were very similar (Fig. 2d).

Figure 4 of McLay (1974) is reproduced here as Fig. 2e, with H_{max} and H' values for fossil assemblages plotted as well. The predicted value for the pre-European fauna ($2.5 = 12$ equally abundant native species with no introduced species; see Fig. 2c) is shown by the intercept of the solid line with the y-axis. All fossil H_{max} values, and two of the H' values were greater than this value. H' for Poukawa 3 (with few small passerines and less deposition time than Poukawa 1 or 2) was at the intercept and only the Otiran fauna at Oparara was smaller.

Species-area relationships

Forest species

The species lists used for the biogeographic analysis are shown in Table 2 and were compiled as follows:

List 1. The 27 forest birds known to be present in the South Island in 1840 are given in the first column of Table 2. Flux (1989) accepted 27 species but did not list them. He in fact included the laughing owl (*Sceloglaux albigifacies*) instead of the falcon (*Falco novaeseelandiae*) (J. Flux, pers. comm. 1990). *Cyanoramphus malherbi*, which is included in the 1970 checklist (Kinsky 1970), is assumed to be a valid species.

List 2. To the 27 species listed in Table 2 are added the kea (*Nestor notabilis*), the kingfisher (*Halcyon sancta*), and the laughing owl (*Sceloglaux albigifacies*). The differences between lists 1 and 2 are not critical, nor is the possible exclusion of *Cyanoramphus malherbi*. That Flux (1989) accepted *Sceloglaux albigifacies* and rejected *Falco novaeseelandiae* (which does not "rely on" forest although it is a well known inhabitant of North Island and West Coast forests (Fox 1978)) is irrelevant to the totals. The higher total (30) including *C. malherbi* is accepted here.

The arguments developed here and in Flux (1989) depend heavily on which species are considered to be forest birds, so some justification for including the three species is desirable.

O'Donnell & Dilks (1986) reported the kea in West Coast forests from lowland forest (rarely) and from the valley floor to the bushline in high country valleys. They were observed in several forest types, including rata, kamahi, and silver beech.

Despite Oliver's (1955) comment that the kingfisher "is more of a bird of the open than of the forest", kingfishers are conspicuous residents of many forest areas, usually near the edge, and along streams, but also "well into forest" (O'Donnell & Dilks 1986). O'Donnell (1981) reported that the foods of kingfishers from three sites included many forest insects. Robertson et al. (1983) included it in a discussion of forest birds from the southern North Island.

Williams & Harrison (1972) suggested that the laughing owl was a bird of rocky areas and the forest edge, but it has been recorded from forested areas of both the North and South islands. Subfossil remains have been found at sites such as Pyramid Valley (Scarlett 1955) where it was associated with a forest avifauna, and where forest was the dominant vegetation at the time of deposition (Burrows 1989). Williams & Harrison (1972) advocated a grassland habitat on the basis of the best-documented records from last century, those of T. H. Potts and W. W. Smith in inland and South Canterbury. In these areas, the birds were associated with rocky ground, and forest remnants.

I suspect that the laughing owl was primarily a forest species and that the abundance of records from grassland areas reflects both the presence of acute observers in those areas, and the ease of observation in forest edge or open habitats. The rocky hillsides of South Canterbury had patches of forest and, as suggested by Williams & Harrison (1972), the fur reported from owl castings was as likely to have been from native bats as from the introduced kiore (*Rattus exulans*). The long-tailed bat (*Chalinolobus tuberculatus*) is still found in the area (Daniel & Williams 1984). In any event, kiore do live in forest.

Plausible arguments can be presented for including other birds, especially the brown teal (*Anas aucklandica*), in this list. Williams (1964) suggests that this duck was originally characteristic of swamp forests of kahikatea (*Dacrydium dacrydioides*), and T. Worthy (unpubl. data) also argues for its inclusion. The addition of this species to List 2 would only strengthen the conclusions of this paper.

List 3. Additional taxa (apart from moas) accepted as forest birds in the pre-human avifauna are shown

the third column of Table 2. Taxa marked with an asterisk (*) are usually accepted as forest birds. Of the remainder, *Porzana tabuensis* is now found in the forest on Aorangi, one of the Poor Knights Islands (Mildenhall 1982). Palaeoecological studies (e.g., Worthy & Mildenhall 1989) and analogy with living or recently extinct species (e.g., *Aegotheles*-Pizzey 1980; Olson et al. 1989) indicate that the species in the third column of Table 2 can be considered to be forest birds. There was a considerable diversity of forest birds in pre-human New Zealand, and some of these have been reduced to relicts or perhaps extinguished by Polynesian fires 600–800 years ago (McGlone 1999). It is reasonable to expect that many bird species preferred, or were confined to, specific forest types, and that not all the species referred to here as forest birds would be expected in a single forest type. Nevertheless, there will always be some disagreement about palaeohabitat requirements for some species, even those such as the takahē (*Porphyrio mantelli*) which are still extant (Mills et al. 1984; Beauchamp & Worthy 1988; Mills et al.

1988). Although we can infer much from the resemblance of a fossil assemblage to present communities, and from knowledge of the habitat available within the catchment area of each site, it must not be overlooked that present communities contain a high proportion of recent immigrants and present populations of indigenous species may be occupying suboptimal, fringe habitat. Species in the pre-human fauna had very different selective pressures placed on them, and usually unknown ecological scope. The presence of rails in forest on predator-free islands suggests that their mainland habitat has contracted through community change and mammalian predation pressure. Other species, such as the rock wren *Xenicus gilviventris*, may well have occupied different habitats before mammalian predators restricted them to closed environments of rockpiles and scrub (Worthy & Mildenhall 1989). List 4. List 4 comprises nine species of moas (Dinornithiformes) found in the South Island. Burrows (1980, 1989); Burrows et al. (1981); Anderson (1982, 1984, 1990); Worthy 1988, 1989b,

Table 2. South Island species accepted as forest birds by Flux (1989) and in this paper. List 1, those present in 1840; List 2, species added in this paper; List 3, species extinct by 1840, but considered to be forest birds in this paper; List 4, South Island moa species. *—usually accepted as forest birds.

List 1	List 2	List 3	List 4
<i>Alcedo australis</i>	<i>Nestor notabilis</i>	<i>Cnemidornis calcitrans</i>	<i>Anomalopteryx didiformis</i>
<i>Alcedo haasti</i>	<i>Halcyon sancta</i>	<i>Eurynas finschi</i>	<i>Megalopteryx didinus</i>
<i>Alcedo oweni</i>	<i>Sceloglaux albigularis</i>	<i>Harpagornis moorei</i>	<i>Emeus crassus</i>
<i>Alcedo australis</i>		<i>Circus (=Accipiter) eylesi</i>	<i>Eurypteryx geranoides</i>
<i>Alcedo novaeseelandiae</i>		<i>Porzana tabuensis</i>	<i>Pachyornis australis</i>
<i>Alcedo habroptilis</i>		<i>Porphyrio mantelli</i>	<i>Pachyornis elephantopus</i>
<i>Alcedo meridionalis</i>		<i>Gallinula hodgsonorum</i>	<i>Dinornis novaeseelandiae</i>
<i>Alcedo novaeseelandiae</i>		<i>Fulica chathamensis</i>	<i>Dinornis struthoides</i>
<i>Alcedo auriceps</i>		<i>Aptornis otidiformis</i>	<i>Dinornis giganteus</i>
<i>Alcedo malherbi</i>		<i>Coenocorypha aucklandica</i> *	
<i>Alcedo lucidus</i>		<i>Aegotheles novaeseelandiae</i>	
<i>Alcedo taitensis</i>		<i>Xenicus gilviventris</i>	
<i>Alcedo novaeseelandiae</i>		<i>Traversia lyalli</i> *	
<i>Alcedo chloris</i>		<i>Pachyptila yaldwyni</i>	
<i>Alcedo longipes</i>		wren n. gen. n. sp.	
<i>Alcedo melanura</i>		<i>Corvus moriorum</i>	
<i>Alcedo novaeseelandiae</i>		+ List 1	
<i>Alcedo igata</i>		+ List 2	
<i>Alcedo australis</i>			
<i>Alcedo macrocephala</i>			
<i>Alcedo capensis</i>			
<i>Alcedo ochrocephala</i>			
<i>Alcedo novaeseelandiae</i>			
<i>Alcedo fuliginosa</i>			
<i>Alcedo carunculatus</i>			
<i>Alcedo cinerea</i>			

Notes: List 1, 27; List 2, 3; List 3, 16 including 6 rails and ducks, i.e., 10 "nonrails"; List 4, 9.

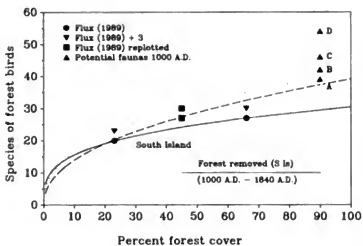


Fig. 3 Species of native forest birds known from New Zealand at A.D. 1000, A.D. 1840, and at present, based on fig. 1 in Flux (1989). Solid line is curve as in Flux's figure; dashed line is this curve replotted to pass a revised point for forest cover and number of species at A.D. 1840 (see text); and dotted line passes through the revised point, using species number from List 2 (see text). The filled triangles represent potential faunas for the whole South Island before man's arrival, comprising: A, List 1 plus species from List 3 which conform with Slud's (1976) definition of land bird, except that *Euryanas fuschii* is included; B, total for A, plus species in List 2; C, total for Lists 1-3, i.e., including all species accepted here as forest birds, except the moas; D, total for C plus all 9 South Island moas.

1990); and Worthy & Mildenhall (1989) have discussed the ecology of moas and suggest that most, if not all, species occupied forests, forest margins, or shrubland, although others, such as Batcheler (1989), have argued otherwise. Only *Pachyornis australis* and perhaps *Megalapteryx didinus* seem to have preferred higher altitudes, above the treeline in some areas. Even there, though, there would have been shrubs and herbs as well as grasses available as food.

Other taxa with claims to have inhabited forest before mammalian predators were introduced include: paradise shelduck (*Tadorna variegata*), by analogy with a species of *Tadorna* which is found in forest, and perches in trees, on some islands near New Guinea (J. M. Diamond, pers. comm.); *Anas aucklandica* (reported by Williams (1964) to have mainly inhabited swamp forest); and *Gallirallus philippensis* (which lives in low forest on small islands near Stewart Island; Kinsky 1970).

Fig. 3 is based on fig. 1 of Flux (1989), but for clarity only the South Island curve is plotted. The x-axis indicates the percentage of land area under forest cover, a value that differs little from the

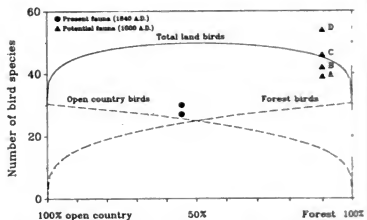


Fig. 4 Number of open-country, forest, and total terrestrial bird species expected and known in New Zealand, against relative proportions of open and forested land. Fig. based on fig. 2 in Flux (1989); present (A.D. 1840) and fossil (A.D. 1000) assemblages, and dotted curve through List 2 1840 value, added. Lettered filled triangles as in Fig. 3.

percentage of original forest cover because the South Island was probably about 85-90% forested in pre-human times (McGlone 1989). In Flux (1989), the point corresponding to number of forest bird species in the South Island in 1840 is plotted at 66% of original forest cover (North Island plus South Islands). I have replotted the point at 45% forest cover because McGlone (1989) has indicated that about 50% of the South Island forest cover present in pre-human New Zealand had been removed by the time Europeans arrived. Species in List 2 are plotted above Flux's values, for both 66% and 45% forest cover. The total number of forest bird species for the South Island, based on but not corresponding to the lists above, are plotted at 90% forest cover.

Point A (Fig. 3, 4) represents a conservative estimate of the number of forest species excluding the moas, the most contentious group: it includes all species in List 1 plus those in List 3, except *Cnemidornis*, *Porphyrio*, *Gallinula*, and *Fulica*. It therefore conforms to Slud's (1976) definition of land birds except for including *Euryanas* for which there is abundant evidence that it was primarily terrestrial. For B, the species in List 2 were added, and C includes also those species omitted on Slud's criteria but regarded here as terrestrial. D represents the total South Island forest avifauna, if all nine species of moa are included.

The curve plotted through Flux's points falls well below the potential values for the whole island, but curves fitted through present and replotted 1840 points pass near the lowest points. Smaller total

forest areas at A.D. 1000 would steepen both curves and bring them closer to the totals predicted here.

Figure 2 of Flux (1989) is reproduced here as Fig. 4. Points corresponding to species number in four potential faunas and the replotted 1840 point shown on Fig. 3 have been added, as well as the line fitted through the higher estimate of 1840 forest bird species. The number of terrestrial species (including those omitted by Slud (1976) in the potential faunas agreed closely with that predicted on the basis of an even mix of forest and open-country species on Flux's original plot. If the open-country and total land bird curves were also replotted, however, assuming equal numbers of forest and open-country species, the total land fauna would reach at least 60 species. Although further species will probably be found, it is unlikely that the total terrestrial avifauna for the whole South Island was greater than 50 species in the Holocene. The number of open-country species did not reach that predicted by the model.

DISCUSSION

I have assumed a direct relationship between the composition of fossil faunas at the four sites and that of the living communities they represent. This represents an ideal situation, unlikely to be approached in practice because of the vagaries of deposition and preservation. The relationship has never, to my knowledge, been studied under New Zealand conditions. The taphonomy of New Zealand fossil sites has only recently come under critical study, and there are few data available on the relative trapping efficiencies of swamps and caves for different bird species. I believe, however, that the trends in the data reflect the actual changes in the avifauna, because most of the biases in the fossil data will lead to an underestimation of both potential (H_{max}) and realised (H') diversity.

Some species which could reasonably be expected to be present and breeding in the catchment area of a deposit are, for unknown reasons, not represented in that fossil assemblage. The rarity of small passerines at Poukawa is an example. Flighted species are generally under-represented in cave and swamp deposits because they either do not enter the fossil trap, or they can readily escape if they do. Flightless species are often over-represented in such deposits, for obvious reasons. When and how long the deposit structure acted as a trap, and its ability to sample the fauna present in the area also produce biases in the record at a site: forest birds may be less well

represented in a swamp deposit than waterbirds, although being abundant only a few tens or hundreds of metres away.

At the Washpool site, both species represented and numbers of individuals were directly related to human dietary preferences (Leach 1979). Chance is also an important factor, as is absolute abundance of a species in the living community. Many fossils of small acanthisitid wrens are known from cave deposits in both main islands, but only two specimens of an undescribed long-billed species have been found so far (P. R. Millener and T. H. Worthy, pers. comms.). Was this bird really rare in the unmodified community that the trap sampled, or did its habits and climbing ability keep it away from caves or enable it to escape from them easily?

The values of H' calculated for fossil assemblages are comparable with those for living faunas, and increased slightly with H_{max} as expected. The lower than expected increase probably resulted from factors such as poor representation of flighted, arboreal, and rarer species and dominance of flightless species. The slightly lower mean evenness value for the fossil assemblages supports this explanation for the lower slope of the combined fossil and present curve, because there is no *a priori* reason to suspect that bird communities in undisturbed forests should have different overall patterns of abundance than present communities. If evenness was higher, H' would have been higher too.

The Shannon Index was shown to be highly correlated with total species number for the fossil assemblages, as expected from other studies. It was used here purely to facilitate direct comparisons with the published work.

McLay's (1974) prediction of $H_{max} = 2.5$ for the diversity of forest birds in the pre-European fauna is too low if "pre-European" is extended to the "pre-human" situation. At any one site and time, the potential H_{max} was up to 3.5, and the realised H' at least 2.1–2.9. Allowing for the biases in deposition, it is clear that the Shannon diversity of New Zealand forest birds has declined over the past 1000 years, although there are still extensive areas of forest remaining, particularly on steep lands.

Even if the relationship between species number and forest area today is accurately modelled by the curve in Fig. 3, the considerable positive deviation from the expected number in the fossil communities must be explained. Either some or all of the extinct species included in the forest bird totals were not forest dwellers, or New Zealand had disproportionately more forest bird species than other islands.

Flux (1989) takes the first view; the second is supported by the paucity of native open-country birds in either the present or fossil assemblages. Compared with the large fauna of obligate grassland birds in Australia, a fauna which includes many parrots and grass finches, the modern New Zealand open-country avifauna is, and was, depauperate. It may be that, contrary to present expectations, the number of extinct passerines has been grossly underestimated (J. M. Diamond, pers. comm.) because the small gauge screens necessary for their detection have not been used routinely in New Zealand excavations. If, as Diamond suggests, the fossil avifauna was twice as large as we presently think, then the apparent lack of open-country species may be an artefact of collecting. Few, if any, sites laid down in open-country (i.e., grassland) have been excavated yet. In any event, such a large increase in extinct taxa would only exacerbate the present difference between biogeographic theory estimates of New Zealand bird diversity, and the empirical data.

Diamond (pers. comm.) also points out that it is very difficult to calculate the expected number of species for a temperate Pacific island of New Zealand's size, because the base work has not been done for Australia and nearby islands. This is not attempted here, because the discussion centres on Flux's use of Slud's analysis, but such a study may well provide new insights into what may be expected, if not in Holocene deposits, then in Miocene and early Pleistocene faunas of New Zealand.

Keas (*Nestor notabilis*) penetrate high altitude fellfields and riverbeds. Pipits (*Anthus novaeseelandiae*) certainly live in tussock grasslands, but it has been suggested that they require taller vegetation in their territories (Bull, in Hamel 1972), or at least higher rainfall or humidity, than the introduced skylark (*Alauda arvensis*) (Hamel 1972). The extinct quail (*Coturnix novaeseelandiae*) was apparently associated with open tussock grasslands. The harrier (*Circus approximans*) can hunt effectively in closed kanuka (*Kunzea ericoides*) forest (pers. obs.; H. Cameron pers. comm.) but prefers grassland; it is rare in deposits older than 1000 years. There is considerable empirical evidence from faunal associations and vegetation prevailing at fossil sites during deposition, that species such as Haast's eagle (*Harpagornis moorei*) and owl-nightjar (*Aegotheles novaeseelandiae*) which Flux and McLay assumed to have inhabited open-country, lived in some forest types. McLay's comment that "It is significant that no native forest birds are known

only from sub-fossil remains", although in keeping with the popular view of the time, is incorrect, as shown, for example, by the acanthisittid wrens.

The point is, that even if we accept half of the moas as open-country birds, the total number of such species will not match that predicted or assumed in the model. Therefore the curves in Fig. 4 will be strongly skewed to the right. Flux's contention, on biogeographic grounds, that many of the extinct species were open-country birds, is not supported by the empirical data on fossil faunal and floral assemblages.

If some groups in the pre-human avifauna were restricted by the small extent of their preferred grassland habitat in the Holocene, they should not have declined as rapidly as they did when the grasslands expanded dramatically 500–800 years ago, even allowing for the intensity of human predation (Anderson 1989). If some or all moas were grassland birds, their habitat increased by several hundred percent. Similarly, the increase in grassland should have increased the habitat available to the takahe (*Porphyrio mantelli*), if it were a true grassland species. There is no firm basis on which to predict that even half of moa species inhabited open-country.

It is here that palaeoautecological studies must take over. Worthy (1990) suggests on distributional and faunal grounds that two of the nine species of moa in the South Island—*Megalapteryx didinus* and *Pachyornis australis*—inhabited open high country habitats. Two others, *Anomalopteryx didiformis* and *Dinornis novaeseelandiae*, were common in the wet western forests during the Holocene. The other species were abundant to the east of the main ranges, in drier forests and shrubland.

Zimmerman & Bieregaard (1986) pointed out in another context that even for living communities, autecological studies often allow far better predictions of presence or species numbers in habitats than do simple species-area relationships.

If we accept that the pre-human avifauna was dominated by forest species, the high rate of extinction in the fauna in the period before European settlement must be related to the characteristics of the forest areas removed in that period. These forests were mainly the drier, eastern forests, or those in inland areas where drought or severe climate restricted regeneration after clearances (McGlone 1980, 1983, 1989). This applies to both main islands. I have discussed this elsewhere (Holdaway 1989) and suggested that it was the drier, more structurally diverse forests on more fertile soils which supported

the greatest diversities of birds in pre-human times. The maximum diversity was attained in western and northern areas only when climatic conditions favoured vegetation other than tall, wet forest. Even in the wetter forests, the fall in diversity of birds probably accompanied, and may have caused, a change in the structure of the forests themselves. As Wardle (1986) noted that "We must now accept that the pre-Polynesian forests of New Zealand could have been as different from the forests of the immediately pre-European era as the latter were from the native forests of today".

The total number of terrestrial bird species in the pre-human fauna agrees closely with Flux's prediction only if rails and ducks are excluded. Hild's (1976) criteria for land birds do not appear to hold for island faunas, particularly where mammalian predators are absent. It may be simpler not to consider groups such as the rails species by species, but these groups bridge the division between terrestrial, and indeed forest habitats and freshwater habitats. Waterfowl, too, can be primarily terrestrial. Even in Australia, where mammalian and reptilian predators are, or were, abundant, the maned goose *Chenonetta jubata* spends much time far from water. Similarly, the Hawaiian goose *Branta sandvicensis* is terrestrial.

It is important to consider each species separately when assessing the palaeohabitats of New Zealand birds. To ignore the rails and waterfowl seriously biases the data in island ecosystems. A better understanding of changes in diversity with time, and of faunal composition and habitat requirements is important, not only for theoretical biogeographical reasons, but as a basis for management of the remaining forest biota.

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The male reproductive system of *Costelytra zealandica* (White) (Coleoptera: Scarabaeidae: Melolonthinae)

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Abstract The morphology and histology of the male internal reproductive organs of *Costelytra zealandica* show many similarities to other Scarabaeidae, and are particularly close to other Melolonthinae and to Rutelinae. Testes follicles of *C. zealandica* have the usual structure for Melolonthinae with basal lobes surrounding the ends of the vasa efferentia. Epithelial cells of the vasa efferentia, vasa deferentia, and vesiculae seminales have similar densely basophilic cytoplasm but muscle layers are best developed around the latter. Accessory glands lack muscle and are not differentiated histologically into regions but do differ from their reservoirs. The ejaculatory duct has a cuticular intima and is differentiated into anterior and posterior regions. Both are surrounded by a muscular sheath which expands in the posterior region to enclose fluid. This forms a hydraulic mechanism for everting the internal sac during intromission. The parameres hook into the female's genital chamber during copulation and have no pincer action. Probable homologies are listed between muscles of the external genitalia and anus of *C. zealandica* and other Scarabaeoidea.

Keywords Coleoptera; Scarabaeidae; *Costelytra zealandica*; morphology; histology; genitalia; muscle anatomy

INTRODUCTION

The male reproductive system of *Costelytra zealandica* (White) has not been described before although diagrams of the internal reproductive organs were published by Fenimore (1971). Elliott (1964) reported testes development and the appearance of other reproductive organ rudiments in the pre-adult and Kelsey (1965) and Kain (1972) gave characters for distinguishing male and female imagines. The female reproductive system was described by Stringer (1988).

Detailed morphology of male internal reproductive organs for other Melolonthinae was published for *Phyllophaga anxia* (Le Conte) by Berberet & Helms (1972), *Amphimallon majalis* (Razoumowski) by Menees (1963), and *Melolontha melolontha* L. by Straus-Dürckheim (1828). In addition, Williams (1945) included descriptions of 7 Scarabaeidae including a melolonthine, and Bordas (1900) includes 6 Melolonthinae together with 23 other Scarabaeidae. Descriptions of male reproductive systems are also available for the rutelines *Phyllopertha horticola* L., *Anomala aenea* Geer, and *Anomala ausonia* Erichs (Lupo 1947; Rittershaus 1927); the scarabaeines *Scarabaeus semipunctatus* F. (Dajoz 1972) and *Coprophanaeus lancia* (L.) (Edmonds 1974); the dynastine *Heteronychia arator* Fabr. (Johannesson 1975); and the passalid *Passalus cornutus* F. (Krause 1946). Hardy (1981) figured the internal reproductive organs of *Adoryphorus coultoni* (Burmeister) (Dynastinae). Histological descriptions are published for *P. anxia* by Berberet & Helms (1972), *A. ausonia* by Lupo (1947), *P. horticola* and *A. aenea* by Rittershaus (1927), two *Cetonia* species (Cetoniinae), two Lucanidae, and a geotrupid by Bordas (1900).

MATERIALS AND METHODS

Beetles were collected from Collins Road, Hamilton, New Zealand by beating from bushes after dark or digging them up. They were anaesthetised with chloroform or carbon dioxide and dissected under

Clarke's Insect Saline (Hale 1965). Transverse and longitudinal serial sections of both entire abdomens and excised organs were made using normal histological techniques (Stringer 1988). Muscle anatomy was examined from a series of progressively deeper dissections. These were fixed lightly with 4% formalin and the muscles stained with repeated washing in dilute Mallory's phosphotungstic acid haematoxylin. Positions of internal organs in copulating beetles were determined by dissecting paired beetles after they were quick frozen in liquid nitrogen and subsequently fixed in boiling Bouin's fixative (Stringer 1988). Scanning electron micrographs of male genitalia during copulation were prepared after dissecting away the female. The male was then freeze dried, attached to an aluminium stud with conducting silver adhesive, sputter coated with a thin film of gold under vacuum and examined with a Philips Stereoscan. Whole mounts were prepared after maceration (Oldroyd 1958).

All drawings were made on graph paper using a squared microscope eyepiece. Measurements were taken with a calibrated eyepiece micrometer.

Terminology

I use the terminology of Lindroth & Palmén (1970) except for a pair of small sclerites on either side of the anus which I refer to as anal sclerites because their homology is uncertain. The aedeagus shows its true relationship with the rest of the body when it is extended during copulation and I use the terms anterior, posterior, left, and right with respect to it in this position irrespective of its secondary orientation within the body while in repose.

THE MALE INTERNAL REPRODUCTIVE ORGANS

The male reproductive organs (Fig. 1) comprise paired testes, two vasa deferentia with vesiculae seminales, a pair of accessory glands with reservoirs, and a ductus ejaculatorius. Each testis consists of six separate follicles connected by vasa efferentia to a vas deferens.

Some dimensions of the reproductive organs are given in Table 1. The vas deferens, seminal vesicles, accessory gland reservoirs, and ejaculatory duct vary considerably in overall size in relation to mated state. Seminal vesicles, in particular, become difficult to distinguish from vas deferens immediately after copulation when they are empty. Changes in size of

accessory gland reservoirs with respect to age and copulation were published by Fenimore (1971).

The testes

Testes follicles are opaque white and roughly spherical except for slightly flattened apical and basal ends. Their apical surfaces are usually held close to lateral regions of the 6th to 8th abdominal segments by tracheae. Five follicles generally surround the sixth but less frequently they form an irregular group of six.

Each follicle is enclosed within an outer sheath about 2 µm thick containing scattered muscle fibres and an inner sheath less than 1 µm thick (Fig. 2A). Both sheaths are invaginated inward by the end of the vas efferens which extends into the centre of the follicle and expands as a conical opening 80–100 µm in diameter (Fig. 2A). The proximal half to two-thirds of the follicle is subdivided radially by septa into 10–14 lobes that are filled with cysts at later stages of spermatogenesis. These lobes are often demarcated externally by slight indentations around the equator of the follicle. Each septum is an invagination of the inner sheath which extends radially through the basal portion of the follicle. Small tracheae also run inward between adjacent walls of the septa. In contrast, the apical region of the follicle is undivided by septa and consists of a thick disc-shaped region of spermatogonia and cysts at early spermatogenesis (Fig. 2B). Some apparently irregular invaginations of the inner sheath occur in the apical region, particularly towards the periphery near the septa. They appear to be shallow but their walls are difficult to follow within the compact apical mass (Fig. 2B). There is no apical invagination as described for Cetoniinae and Dynastinae by Virkki (1957). Some apparently incomplete and irregularly folded membranes and epithelial cells occur beneath the apical region of *C. zealandica*. These are situated near the opening of the vas efferens and are separated from it by cysts of spermatozoa. No signs of degeneration were found amongst these epithelial cells, as reported in some Melolonthinae and other Scarabacidae by Virkki (1957).

The vasa efferentia

The vasa efferentia are very elastic, thin transparent ducts. Each consists of a layer of cuboidal to columnar epithelial cells, 4–10 µm high, resting on a basement membrane (Fig. 3A). The cells have a smooth inner border but distinct intercellular walls are only visible with phase contrast. Their cytoplasm is densely and

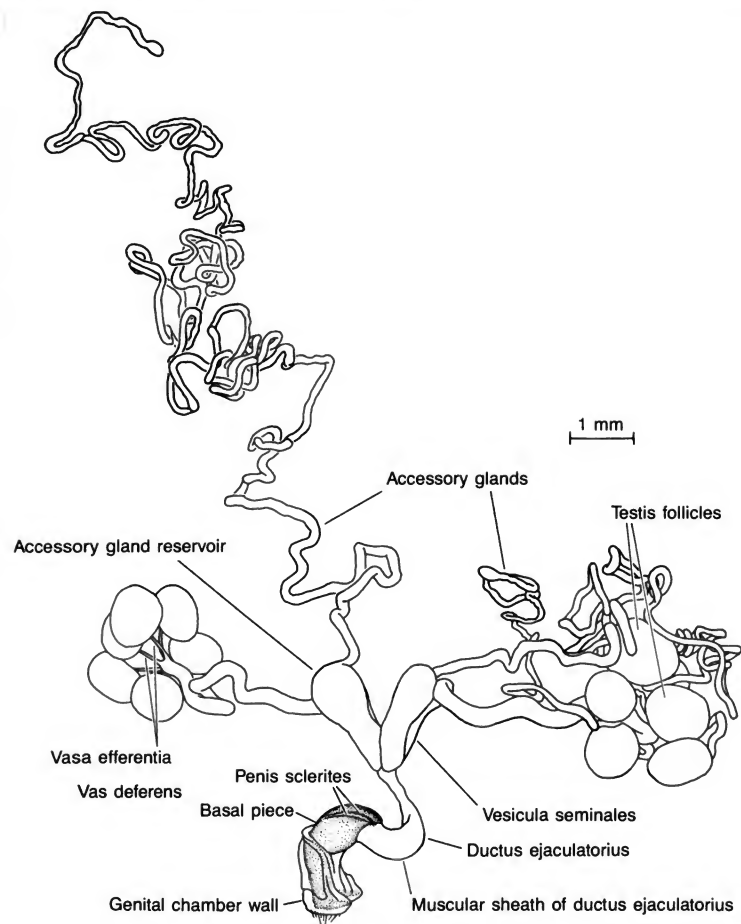


Fig. 1 Male reproductive organs of *Costelyia zealandica* after removal from the beetle. Dorsal view with the left accessory gland unraveled.

Table 1 Dimensions of male reproductive organs of *Costelytra zealandica* (from 10 field collected specimens).

		Mean (mm)	SD (mm)	Range (mm)
Testis follicle	Max. diameter	0.77	0.26	1.10–0.37
Vas deferens	length	7.09	0.98	8.27–5.33
	width	0.28	0.04	0.33–0.10
Accessory gland	length	60.3	6.4	73–52
	width	0.17	0.03	0.23–0.07
Accessory gland reservoir	max. width	0.41	0.08	0.60–0.33
Seminal vesicle	max. width	0.29	0.01	0.43–0.20
Combined accessory gland reservoir and seminal vesicle	length	1.46	0.21	1.77–1.17
Anterior region of ejaculatory duct	length	2.06	0.41	2.50–1.17
	width	0.19	0.06	0.32–0.13
Muscular sheath of ejaculatory duct external to tegmen	length	1.99	0.35	2.73–1.80
	width	0.59	0.11	0.87–0.47
8th sternite + spicules	max. length	1.28	0.14	–
basal plate	length	2.14	0.12	–
	max. width	1.05	0.07	–
Paramere	length	1.01	0.07	–

evenly basophilic and their nuclei are rounded and basal. A thin reticulum of predominantly longitudinal muscle fibres surrounds these organs.

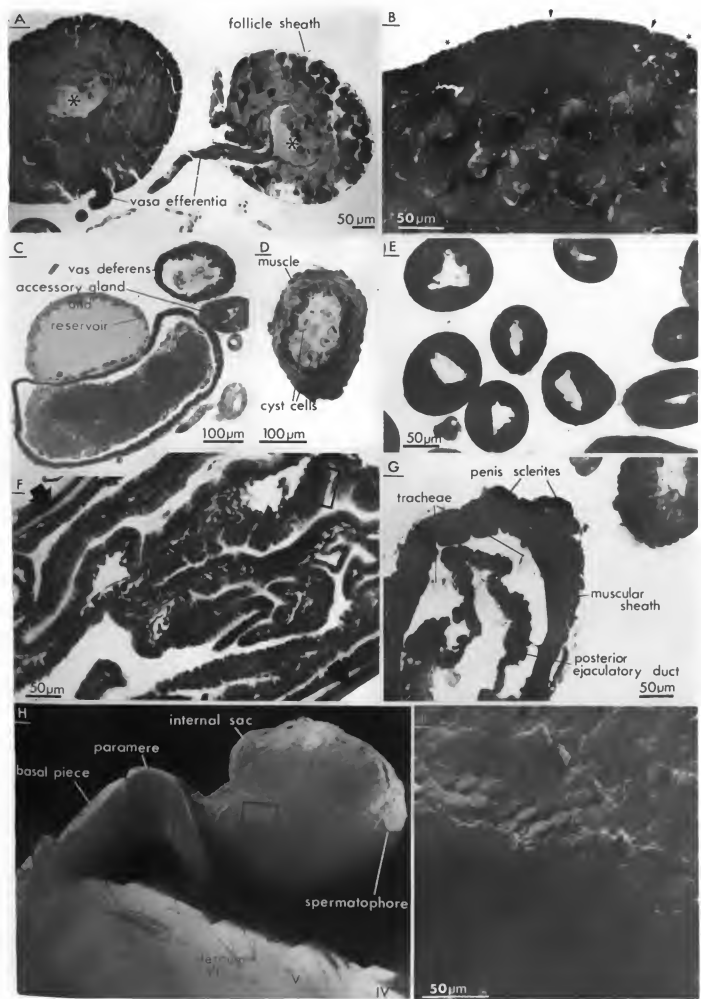
The vasa deferentia and vesiculae seminales

The vas deferens and seminal vesicles appear opaque white because of secretions and spermatozoa within them. They may also have small translucent white patches where their contents are clearer. The distal end of each vas deferens is located medial to its cluster of testes follicles. It twists and coils irregularly towards the midline then dilates into a seminal vesicle. Both seminal vesicles run parallel to each other but do not usually touch until they join the ejaculatory duct (Fig. 1). Each seminal vesicle also lies ventral to an accessory gland reservoir and is

bound to it by a thin sheath containing scattered longitudinal muscle fibres. The combined seminal vesicles and accessory gland reservoirs lie ventral to the rectum and medially or slightly towards the right within the fifth to sixth abdominal segments. They also lie at an angle with their distal ends directed anterior-ventrally and their proximal ends posterior-dorsally.

Vas deferens and seminal vesicles both have an epithelium of flattened to columnar cells 6–25 µm tall. These rest on an outer basement membrane, have rounded or bulging inner surfaces and indistinct intercellular membranes (Fig. 2C,D, 3B). Their cytoplasm is basophilic with a darker-staining network of strands that become sparser and branch less frequently apically. No vacuoles were visible.

Fig. 2 Photomicrographs of male reproductive organs of *Costelytra zealandica*. (A) Section through two testis follicles. Both are packed with cysts of spermatids or spermatozoa. The section passes through the funnel-like openings of the vasa efferentia (asterisks) but does not pass through the apical regions of the follicles; (B) Section through the apical region of a testis follicle. The apical region extends approximately between the asterisks and the arrows indicate where the inner sheath forms shallow invaginations. Cysts of spermatozoa and later stages of spermatogenesis pack the testis follicle below the apical region; (C) Transverse section through an accessory gland reservoir and a seminal vesicle. The sheath binding these together is not present in this section. Also visible in transverse section are an accessory gland and the posterior part of the vas deferens; (D) Transverse section through a vas deferens; (E) Transverse sections through an accessory gland; (F) Longitudinal section through the posterior end of the basal piece containing the withdrawn internal sac. The scale-like ornamentation of the inner sac (shown in Fig. 2I) is only distinguishable occasionally (such as within the black frame). Portions of basal piece cuticle are indicated by black arrows; (G) Transverse section through anterior (upper right) and posterior (lower left) regions of the ejaculatory duct. Note the cavity between muscular sheath and posterior ejaculatory duct; (H) Scanning electron micrograph of male genitalia in copula after removal of the female. The internal sac is starting to withdraw from the spermatophore but its retreating edge (black arrows) is mostly obscured by secretion. Abdominal sternum numbered IV to VIII; (I) Scanning electron micrograph of the triangular scale-like processes on the internal sac. This is a higher magnification of the framed portion in Fig. 2H.



These epithelial cells flatten when the organs dilate with secretion but when empty or nearly empty the seminal vesicles become thrown into longitudinal folds which are less frequent next to the accessory gland reservoirs. A layer of well separated circular to oblique muscle fibres surrounds the vas deferens, (Fig. 2D). This thickens into three or more distinct layers around the vesiculæ seminales.

The secretion within the vas efferens, vas deferens, and seminal vesicles contains a tangled mass of mostly separate spermatozoa together with large rounded cells (Fig. 2C,D). The latter have eosinophilic cytoplasm and lightly-staining rounded nuclei and they usually lie peripherally to the spermatozoa in the vas deferens and seminal vesicles. Anderson (1950a) suggests that similar cells in *Popillia japonica* Newman are cyst cells that have accompanied the spermatozoa from the testes and reports that they disintegrate in the female. These cells were not found in spermatophores within female *C. zealandica* (Stringer 1988).

The accessory glands and their reservoirs

The accessory glands coil irregularly within the posterior half of the abdomen (Fig. 1). Proximally, they dilate into short, slightly curved reservoirs that run side by side with seminal vesicles as described above. Accessory glands are usually transparent but may become translucent white with secretion. Their reservoirs are usually more opaque because of the larger volume of secretion they contain. Neither organs are ever as opaque nor as white as vasa deferentia and vesiculæ seminales.

Accessory glands vary from round through oval to almost flattened in cross-section (Fig. 2E; 3C). No muscle fibres surround them. Their epithelial cells are columnar and usually 65–80 µm in thickness but can occasionally vary from 10.5–90 µm. Often, up to five longitudinal rows of taller epithelial cells project as low ridges into the lumen of the gland. All cells have smooth apical surfaces, indistinct intercellular membranes, densely basophilic cytoplasm with occasional small vacuoles, and central nuclei about 10 µm across packed with granular chromatin. These glands cannot be clearly differentiated into histological regions as Anderson (1950b) did in the ruteline *P. japonica*. Histological differences in the latter were, however, slight and the regions were more clearly recognised histochemically.

Accessory gland reservoirs differ histologically from accessory glands. Their walls vary from 4.5–12 µm thick depending on how distended these organs are (Fig. 2C; 3D). When relatively empty, the

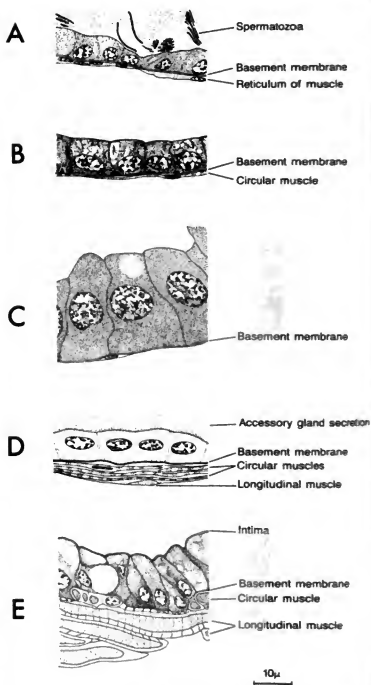


Fig. 3 Histology of the male reproductive organs of *Costelytra zealandica*. (A) Longitudinal section through a vas efferens; (B) Longitudinal section through a vas deferens; (C) Transverse section through an accessory gland; (D) Transverse section through an accessory gland reservoir; (E) Transverse section through the anterior region of the ejaculatory duct.

dorsal and lateral walls become folded longitudinally whereas few folds occur adjacent to seminal vesicles. The epithelial cells have eosinophilic cytoplasm with apical surfaces that are sometimes difficult to distinguish from secretion within the gland. Intercellular walls are distinct only under phase contrast, and the central nuclei are oval. One to five or more layers of circular or slightly oblique muscle envelop closely the reservoirs.

The ductus ejaculatorius

The ejaculatory duct consists of two regions which are demarcated by two large tracheae that enter dorsally. The posterior region is surrounded by a muscular sheath containing two dorsal penis sclerites. These extend over the posterior half of the sheath and are then continued to its anterior end as thin straps of unsclerotised cuticle (Fig. 2G; 4A,B). The portion of muscular sheath containing the penis sclerites also lies within the basal piece.

Most of the ejaculatory duct and its muscular sheath is opaque white although less so than seminal vesicles. In addition, the inner and outer walls of the inner sac usually show through the posterior ventral walls as yellow-brown and brown areas, respectively. When in repose, the ejaculatory duct runs posteriorly for about 1 mm from its anterior end before curving first to the left and then ventrally until it lies to the left in the abdomen. Here it is directed postero-laterally to the right and enters the basal piece. In addition, the muscular sheath of the ejaculatory duct is also twisted through 90° to the right before entering the basal piece but it straightens out and untwists when the tegmen is extended during copulation.

The entire ejaculatory duct is lined by thin intima secreted by a cuboidal to columnar epithelium (Fig. 2G; 3E). Both are folded longitudinally by surrounding muscle layers and the epithelial cells may be stretched or compressed as a result. The surrounding basement membrane often becomes secondarily folded into small longitudinal wrinkles where it is compressed and here the intercellular membranes become complexly folded. Epithelial cells vary from 5–12.5 µm high when undistorted, their nuclei are basal and their cytoplasm is basophilic with darker strands and numerous distal vacuoles. The latter occasionally occupy much of the space within the cell (Fig. 3E). The anterior region of the ejaculatory duct is surrounded by an inner single layer of scattered longitudinal muscle fibres and an outer thick layer of circular muscle. Anteriorly, the circular muscle extends over the ends of the seminal vesicles and accessory gland reservoirs to form a sphincter. Posteriorly, the circular muscle thickens to form the muscular sheath which is separated from the ejaculatory duct (Fig. 2G). This sheath encloses a fluid-filled cavity containing the folded ejaculatory duct and internal sac.

THE EXTERNAL GENITALIA

The aedeagus comprises paired penis sclerites, a tegmen consisting of a basal piece and two distal

parameres, and a largely unsclerotised internal sac (Fig. 4A,B). Given (1952) illustrated the tegmen of *C. zealandica* and used its symmetrical parameres as a taxonomic character.

The external genitalia are partly internal and partly lie within a genital chamber of arthrodial membrane between the 8th tergum and sternum. The genital chamber is a shallow oval cavity with a pair of anal sclerites located dorsally on either side of the anus. It also has a transverse mound on its anterior ventral wall supported by the posterior edge of the 9th sternite. Bristles from the latter are directed towards the opening of the genital chamber. The lateral walls of the genital chamber on either side of the 9th sternite are supported by posterior ends of the spicules. The anterior ends of the spicules constitute the lateral edges of a tongue-shaped genital apodeme invaginated from a slit beneath the 9th sternite. Given (1952) referred to this apodeme as the inner ventral plate. It is a flattened sac with membranous dorsal and ventral walls. A second flattened sac, the dorsal branch of the genital apodeme, extends from the dorsal surface of the genital apodeme and tapers anteriorly. The spicules provide stiffening to resist compression and some twisting when the retractors of the tegmen and oblique rotators of the tegmen (described below) retract the tegmen. In contrast, the thin-walled dorsal branch of the genital apodeme only takes tension from the protractors of the tegmen.

The genital chamber wall dorsal to the 9th sternite and between the ends of the spicules forms the second connecting membrane. It invaginates into a large thin-walled cavity which accommodates the posterior end of the tegmen. This connecting membrane is reflected posteriorly beneath the tegmen and joins the proximal and anterior surfaces of the parameres. Here it completes the ventral part of a tube with the posterior third of the basal piece and provides flexibility for movement of the intrinsic muscles of the tegmen.

The basal piece is somewhat asymmetrical (Fig. 4B) and articulates with the slightly curved parameres at its posterior ventral corners. When in repose, the tegmen lies on its right side (Fig. 6A,B) with its posterior end towards the right and parameres directed postero-laterally. During copulation it rotates back until it is more or less aligned with the axes of the beetle except that the posterior end of the tegmen is directed somewhat ventrally. The parameres and about a third of the basal piece also project out from the abdomen during copulation (Fig. 2H; 6C).

The penis consists of two long thin sclerites (Fig. 4A,B) lying dorsally and alongside each other within

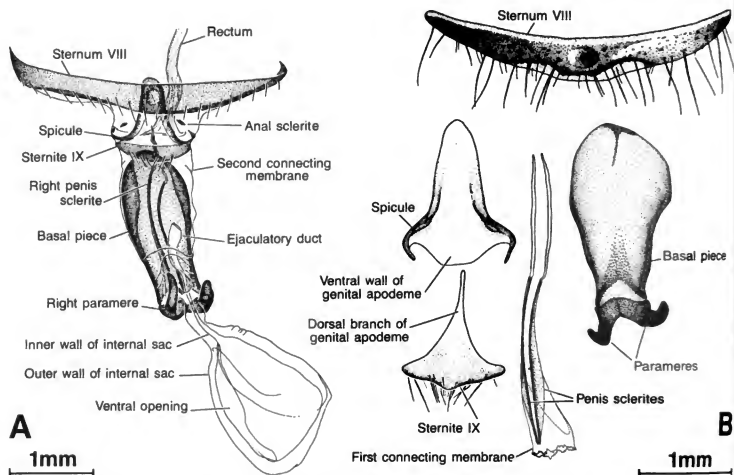


Fig. 4 Male external genitalia of *Costelytra zealandica*. (A) Whole mount of the external genitalia and 8th sternum after maceration (ventral view). Some folds of the internal sac omitted for clarity; (B) The 8th sternum (ventral view) and separated sclerites of the external genitalia (dorsal view).

the muscular sheath surrounding the ejaculatory duct. They merge into anterior flexible strips of cuticle as described above. The penis sclerites prevent the muscular sheath of the ejaculatory duct from shortening during contraction and when the retractor of the internal sac contracts. Their reduction to thin struts, however, allows the muscular sheath to change diameter. Posteriorly, the penis sclerites are broadly attached by unsclerotised first connecting membrane to the outer wall of the internal sac and to the tegmen between the bases of the parameres.

The internal sac fills the bursa copulatrix during copulation. When extended it forms a globular double-walled organ with its opening directed slightly ventrally (Fig. 2H; 4A). Its outer surface is entirely covered with small triangular scale-like processes of slightly stiffened cuticle that point posteriorly (Fig. 2I). The inner wall follows the shape of the outer wall but it lacks scale-like ornamentation. It terminates anteriorly at the ejaculatory duct. When withdrawn, the internal sac collapses and folds mostly

within the posterior ventral part of the muscular sheath surrounding the ejaculatory duct (Fig. 2F). Here, its morphological posterior and ventral regions tend to lie anterior to the remainder whereas the anterior part sometimes projects a small way past the penis or from the tegmen.

MUSCLES OF THE EXTERNAL GENITALIA AND ANAL REGION

The genital and anal muscles of *C. zealandica* are named here according to their supposed function. Genital muscles are grouped into extrinsic muscles which lie outside the tegmen, and intrinsic muscles which lie entirely within it.

The walls of the genital chamber in *C. zealandica* are surrounded by a thin layer of muscle fibres that run in all directions. Some attach to sclerites in the genital chamber but they are only considered to be separate muscles if they form distinctive groups that can be located in every male.

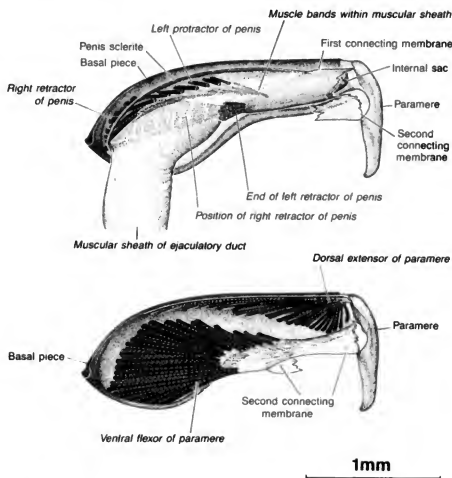


Fig. 5 Intrinsic muscles of the aedeagus of *Costelytia zealandica*. (Upper) Aedeagus viewed from left after removal of left side of the tegmen. The ventral flexor and dorsal extensor of the right paramere are omitted for clarity; (Lower) Sagittal section of the tegmen viewed from the left after removal of the ejaculatory duct, penis sclerites and internal sac and their associated muscles. The right retractor of the penis joins the basal piece immediately antero-medially to the ventral flexor of the paramere.

Intrinsic muscles of the phallus

The dorsal extensors of the parameres (Fig. 5) are two fan-shaped muscles that run from the inner anterior-dorsal and lateral surfaces of the basal piece and insert on the medial dorso-lateral edges of the parameres.

The ventral flexors of the parameres (Fig. 5; 6A,C) are two large muscles that originate on the inner antero-lateral surface of the basal piece and insert on the second connecting membrane close to the parameres. These run on either side of the ejaculatory duct sheath and are the most ventral muscles visible in the basal piece.

The protractors of the penis (Fig. 5) are a pair of flat muscles originating about midway along the lateral edges of the basal piece and inserting antero-laterally on the penis sclerites.

The retractors of the penis (Fig. 5) are flat, slightly tapering sheets of muscle that insert ventro-

laterally on the first connecting membrane where it joins the muscular sheath of the ejaculatory duct. Their origin on the basal piece is medial to the ventral flexors of the parameres.

The muscular sheath of the ejaculatory duct (Fig. 2G; 5; 6A,B,C) is a complex of circular to diagonal muscles which forms a tube around the posterior region of the ejaculatory duct and is only attached to it anteriorly. A thickening of circular fibres at the level of the anterior ends of the penis sclerites acts as a sphincter. In addition, a pair of muscle bands insert onto the anterior tips of the penis sclerites and run posteriorly and obliquely within the outer surface of the muscular sheath towards its anterior ventral region (Fig. 5). These compress the ejaculatory duct longitudinally.

The retractor of the internal sac (not figured) comprises a large number of scattered muscle fibres that originate on the anterior ventral surfaces of the

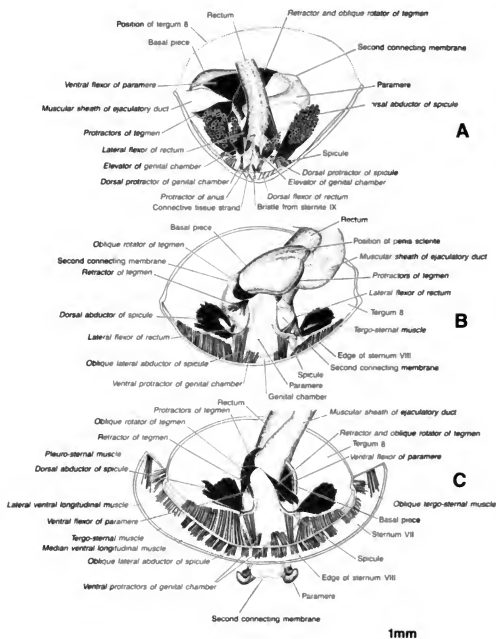


Fig. 6 Musculature of the male external genitalia of *Costelytra zealandica*. Organs are shown in situ after removal of more anterior structures. Muscle names are given in *italics* and abdominal muscles are indicated by dotted lines. (A) Dorsal view after removal of 8th tergum. The aedeagus is shown in repose but its anterior end has moved slightly posteriorly and towards the left. Abdominal sterna omitted for clarity; (B) Postero-dorsal view with aedeagus in repose after removal of 7th sternum; (C) Posterior view during copulation and after the female was dissected away. The everted internal sac is omitted.

penis sclerites and insert on the dorsal surface of the inner wall of the internal sac.

The muscular lining of the internal sac (Fig. 2F) is a dense but thin plexus of muscle lining the internal sac. Its fibres form a reticulum except near the junction with the ejaculatory duct where they tend to run predominantly in inner circular and outer longitudinal layers.

Extrinsic muscles of the phallus

The protractors of the tegmen (Fig. 6A,B,C) are a pair of muscles that originate on the anterior lateral sides of the dorsal branch of the genital apodeme. They run close together around the right side of the ejaculatory duct and insert on the anterior edge of the basal piece slightly towards its right hand side.

The retractors of the tegmen (Fig. 6A,B,C) are a pair of muscles originating on the dorso-lateral edges of the spicules and inserting on the wall of the invagination of the genital chamber medio-laterally to its junction with the tegmen. The oblique rotators of the tegmen (Fig. 6A,B,C) are a pair of muscles that insert dorso-laterally on the wall of the invagination of the genital chamber medial to its junction with the tegmen. They originate anteriorly on the anterior ends of the spicules, prior to the origins of the retractors of the tegmen. The dorsal abductors of the spicules (Fig. 6A,B,C) are a pair of large muscles that insert on the posterior dorso-lateral edges of the spicules and radiate to the posterior dorso-lateral origins on the 8th tergum. The oblique lateral abductors of the spicules (Fig. 6B,C) are paired muscles that each insert medially on a postero-ventral side of a spicule and the 8th sternum near its attachment with the genital chamber membrane.

The dorsal protractors of the spicules (Fig. 6A) are short and very fine muscles. Each originates on the 8th tergum where it joins the genital chamber and inserts dorsally on the postero-lateral edges of the basal arms of the spicules.

The ventral protractors of the genital chamber (Fig. 6B,C) are a small pair of muscles that originate on the 8th sternum near its attachment with the genital chamber membrane but medial to the retractors of the spicules. They insert on the genital chamber membrane between the posterior ventral of the spicules.

Anal muscles

The lateral flexors of the rectum (Fig. 6A) originate on the posterior edges of the dorsal tips of the spicules and insert laterally on the rectum.

The dorsal flexors of the rectum (Fig. 6A) originate on the anterior tips of the anal sclerites then anteriorly to insert on the posterior dorso-lateral faces of the rectum.

The elevators of the genital chamber (Fig. 6A) are large muscles that originate on the 8th tergum and insert on the anterior tips of the anal sclerites anterior to the dorsal flexors of the rectum.

The dorsal protractors of the genital chamber (Fig. 6A) are small muscles that originate on the 8th tergum where it joins the genital chamber membrane and insert anteriorly on the anal sclerites posterior to the elevators of the genital chamber.

The protractors of the anus (Fig. 6A) are two very small muscles that originate on the 8th tergum

medial to the origins of the protractors of the genital chamber. Their insertions are close together on the genital chamber wall dorsal to the anus.

A pair of fine muscles (not figured) were sometimes visible running from the anterior tips of the anal sclerites to the median dorsal wall of the genital chamber anterior to the insertions of the protractors of the rectum. They were not distinguishable from the muscular sheath surrounding the genital chamber in all males even though there are distinct muscles in this position in female *C. zealandica* (Stringer 1988) and in male *Melolontha melolontha* (Straus-Dürckheim 1828) (Table 2).

MECHANICS OF COPULATION

Mating is described in detail by Stringer (1977). Soon after locating a female the male extends the tegmen until parameres and about a quarter of the basal piece project posteriorly from the abdomen. The male then mounts and orientates parallel to the female. Eventually the parameres and end of the basal piece are inserted into the female's genital chamber. The pair become firmly united and the male often loses tarsal contact to be carried about attached only by the tegmen. The probable part played by the female during copulation is discussed by Stringer (1988).

The tegmen is extended from the abdomen principally by contraction of the protractors of the tegmen assisted slightly by the dorsal protractors of the spicules, the oblique lateral abductors of the spicules, and the ventral protractors of the genital chamber. The latter three muscles help by compressing the genital chamber posteriorly, but their main function is to adjust the angle of the tegmen and expand the male genital chamber to facilitate extension and rotation of the tegmen. Straightening and rotation of the tegmen from its resting position are accomplished by the oblique rotators and retractors of the tegmen. These act through the intervening second connecting membrane. The protractors of the tegmen automatically help this rotation when they contract because they are asymmetrically attached to the anterior end of the basal piece.

During extension of the tegmen, the parameres are swung posteriorly through 30–40° by contraction of their dorsal extensor muscles. The medial insertions of these muscles also results in the tips of the parameres being brought close together as they are swung backwards. This aids their exit from the

Table 2 Probable homologous muscles of the external genitalia and anus in male Melolonthinae (from published descriptions). Muscle names are those of the original authors. Muscles of doubtful homology are in square brackets. The dorsal constrictors of the genital chamber (within brackets) are not visible in all male *C. zealandica*.

Muscle number	<i>Costelytra zealandica</i> (White)	<i>Melolontha melolontha</i> L. Straus-Dürckheim (1828)	<i>Amphimallon majalis</i> Razoumowski Menees (1963)
Extrinsic muscles of the aedeagus			
1	Protractors of tegmen	L'Extracteur de l'épui de la verge	Protractors of phallobase apodeme and genital chamber
2	Retractors of tegmen	Le Prétracteur de la gaine de la verge	Oblique rotator of genital chamber
3	Oblique rotators of tegmen	L'Abaisseur de la pièce anale inférieure	Retractors of genital chamber
4	Oblique lateral abductors of spicules	[Le Retracteur antérieur de la pièce anale inférieure]	[Ventral protractor of genital chamber and spiculum gastrale]
5	Ventral protractors of genital chamber	Le Rotateur du cloaque	Ventral protractor of genital chamber and spiculum gastrale
6	Dorsal abductors of spicules	L'Élevateur de la pièce anale inférieure	Oblique lateral abductors of spiculum gastrale
7	Dorsal protractors of spicules	Le Retracteur postérieur de la pièce anale inférieure	Dorsal abductors of spiculum gastrale
8	Dorsal protractors of second connecting membrane	Le Retracteur de la gaine de la verge	Oblique protractor of genital chamber
Intrinsic muscles of the aedeagus			
9	Ventral flexors of parameres	Le Fléchisseur de la pince de la verge	Ventral flexor of phallobase
10	Dorsal extensors of parameres	L'Extenseur de la pince de la verge	Dorsal flexor of phallobase
11	Protractors of penis	L'Extracteur de la verge	[Protractors of aedeagus and endophallic chamber]
12	Retractor of penis	L'Intracteur de la verge	Retractor of aedeagus and endophallic chamber
13	Retractor of internal sac	Le Muscle éjaculateur	-
14	Muscular lining of internal sac	Le Constricteur du prépuce	-
15	-	-	Constrictor of aedeagus and endophallic chamber
16	Muscular sheath of ejaculatory duct	Le Constricteur du canal éjaculatoire	-
Anal muscles			
17	Lateral flexors of rectum	Le Fléchisseur latéral du rectum	Dorsal flexors of rectum
18	Elevators of genital chamber	L'Élevateur du cloaque ou de l'anale supérieure	[Elevator of rectum]
19	Dorsal flexors of rectum	L'Abaisseur du rectum	-
20	Dorsal Protractors of genital chamber	Le Retracteur du cloaque	[Depressor of rectum]
21	Protractors of anus	-	-
22	(dorsal constrictors of genital chamber)	Le Dilatateur de l'an	Constrictor of genital chamber
23	-	-	-
24	-	Le Transverse du cloaque	-

and their entry into the female. Once in the male, the parameres stretch the walls of the female's anal chamber into dorsal pockets on either side of rectum. The parameres are then flexed ventrally slightly anteriorly to the basal piece by their lateral flexors pulling on the second connecting membrane where it is reflected under the basal piece. The parameres are thereby hooked behind the male's 8th tergum. The insertions of the ventral muscles of the parameres do not result in a pincer-like action but their hooking action is assisted by the basal piece being held at a slight angle ventral to the female. The basal piece is held firmly within the male by the oblique lateral rotator and lateral retractor muscles of the tegmen and by contraction of the pro-sutural muscles of the 8th segment. The latter hold the basal piece between sternum and tergum. Once the tegmen is inserted into the female, the male everts the internal sac into the bursa copulatrix. A spermatophore is then formed entirely within the internal sac before the latter is retracted. The following suggestions on how the internal sac is retracted are largely conjectural because few of the muscles involved act on sclerites.

The internal sac is probably extended initially by fluid from within the muscular sheath of the ejaculatory duct. This fluid is forced between the inner and outer walls of the internal sac by contraction of the muscular sheath. The reduction in volume within the muscular sheath occurs because of both a reduction in its diameter as well as a shortening prior to the penis sclerites. A small amount of fluid compression results when the penis sclerites are bent ventrally by contraction of their dorsal retractors. These muscles also slide the penis sclerites a small distance posteriorly from the tegmen; the short first connecting membrane prevents fluid from emerging far. In the copulatory position, the posterior ends of the penis project anteriorly and slightly dorsally relative to the female so it is likely that they help locate the opening to the bursa copulatrix when they contact the dorsal wall of the vagina during intromission (Stringer 1988). Final expansion of the internal sac within the bursa is probably accomplished when fluid spermatophore reservoirs are pumped into it. These inflate the internal sac pressing its inner and outer walls together. It is not known whether the spermatophore gels before the internal sac is withdrawn because unfixed sclerites were not dissected at this stage of copulation.

Movements of the internal sac brought about by muscular lining also probably assist intromission. Only non-copulating males were dissected live and

in these peristaltic waves were initiated at the posterior lip of the internal sac and progressed anteriorly as narrow ripples. Only one wave was visible at a time and the small spines covering the outer wall of the internal sac were momentarily swung to point anteriorly as each wave passed beneath them.

The internal sac is pulled back into the muscular sheath of the ejaculatory duct by its retractor muscle. The penis retractor muscle also pulls the penis and base of the internal sac further back within the basal piece. Retraction and folding of the internal sac is probably assisted by its muscular lining, especially its longitudinal fibres.

Withdrawal of the tegmen is accomplished by the retractors of the tegmen and its oblique rotators. These pull the tegmen in by means of the second connecting membrane. The parameres project ventrally from the basal piece and cannot be swung fully backwards so the tegmen is rotated onto its right side before being withdrawn. This action is largely brought about by the asymmetrical insertions of the tegmen protractor muscles but it may also be assisted by uneven retraction of left and right tegmen retractors and oblique rotators.

DISCUSSION

Most male internal reproductive organs described for Scarabaeoidea are similar to those in *C. zealandica*. The differences that do occur include two or three pairs of accessory glands, two pairs of seminal vesicles, an anterior bulbous extension to the ejaculatory duct, an ejaculatory duct diverticulum, a lack of accessory gland reservoirs or seminal vesicles, or variations in the positions of these storage organs (Bordas 1900; Rittershaus 1927; Krause 1946; Edmonds 1974; Johannesson 1975).

Most Scarabaeoidea have six follicles per testis as in *C. zealandica* although Rutelinae, Cetoniinae, Scarabaeinae, Passalidae, and Lucanidae can have between 2 to 12 per testis (Bordas 1900; Rittershaus 1927; Williams 1945; Krause 1946; Edmonds 1974). In general, the number of testis follicles corresponds with the number of ovarioles except in Scarabaeinae which have only a single ovary with one ovariole (Halfpenny & Lopez-Guerrero 1977). The follicles of an insect testis are typically enclosed within a sheath (Davey 1985) although none are reported in adult Scarabaeidae except in the scarabaeines *Coprophanaeus lancifer* and *Sisyphus schäfferi* L. (Virki 1957; Edmonds 1974). Berberet & Helms (1972), however, report that testes of the melolonthine

Phyllophaga anxia develop within sheaths that later disappear and it also appears likely that such a sheath encloses the testes of immature *C. zealandica* from Elliott's (1964) figures. In other respects the structure of the testes follicles of *C. zealandica* corresponds with Virkki's (1957) middle group (group II) of Scarabaeoidea.

The histology of the internal reproductive organs of *C. zealandica* varies little from other Scarabaeidae. Minor differences include granular cytoplasm of the vasa efferentia and vas deferens, a lack of muscle around these organs, and protoplasmic processes arising from epithelial lining of the accessory glands (Bordas 1900; Rittershaus 1927).

Detailed descriptions of male genital muscles are available for the melolonthines *Amphimallon majalis* (Menees 1963) and *M. melolontha* (Straus-Dürckheim 1828), and for the geotrupid *Geotrupes stercorosus* Scriba (Hieke 1966). In addition, the extrinsic phallic muscles of the scarabaeine *C. lancifer* are given by Edmonds (1974) and mostly intrinsic muscles are described in the rutelines *P. horticola*, *Anomala aenea*, and *Anomala ausonia* by Rittershaus (1927) and Lupo (1947).

Most genital muscles in *C. zealandica* correspond with muscles in the two other Melolonthinae although in five instances a single muscle in one species appears to be represented by more than one muscle in another species (Table 2). In addition, "Le Retracteur antérieur de la pièce anale inférieure" in *M. melolontha* has a more anterior sternal attachment than the corresponding muscle in other melolonthines, and the "protractor of the aedeagus and endophallic chamber" in *A. majalis* attaches to the parameres instead of to the basal piece. Menees (1963) also describes nothing in *A. majalis* comparable with the "muscular sheath around the ejaculatory duct" or "retractor of the internal sac" in *C. zealandica*, and the "constrictor of the aedeagus and endophallic chamber" in *A. majalis* has no clear homologue in the other melolonthines although it appears to be homologous with the "Musculus phallobasicus internus" in the geotrupid *Geotrupes stercorosus* (Hieke 1966) (Table 3).

There appear to be many homologues between the genital muscles of male melolonthines and other Scarabaeoidea although the descriptions are incomplete except for *G. stercorosus* (Hieke 1966) (Table 3). Even in the latter there are only six extrinsic and seven intrinsic muscle differences with melolonthines. Four of the latter are additional muscles concerned with retracting the penis. They are attached to the same sclerites as the protractors

of the penis in Melolonthinae and are therefore possibly homologous even though their origins are more anterior than the protractors of the penis and their functions are antagonistic to them.

Most anal muscles of *C. zealandica* correspond with those of *M. melolontha* but there are fewer evident homologies with those of *A. majalis* (Table 2). The latter differences appear largely because of a lack of anal sclerites in *A. majalis* (Menees 1963). Anal muscles are described for only one other scarabaeid, *G. stercorosus*, by Hieke (1966) and none correspond with those in melolonthines unless "IX. Tergum" in *G. stercorosus* is homologous with the anal sclerites of Melolonthinae. If this is so, then the "M. Antecosta-antecostalis uronotum medialis", "M. uronoto-antecostalis", and "M. tergo-paratergalis" of *G. stercorosus* appear to correspond respectively with muscles 19, 21, and 23 in Melolonthinae (Table 2). However, this still leaves five anal muscles in *G. stercorosus* that cannot be easily homologised with those in Melolonthinae.

The mechanics of copulation were previously described fully for only one other scarabaeid, *A. majalis*, by Menees (1963). Homologous muscles (Table 2) move the tegmen in a similar way to *C. zealandica*. This also applies to the parameres which are fused together but are still flexed during copulation to aid attachment to the female in much the same way as the tegmen in *C. zealandica*. Menees (1963) reports that the internal sac of *A. majalis* is everted by seminal fluid being pumped into it and Rittershaus (1927) describes the same in *P. horticola*. Neither author mentions fluid from within a muscular sheath surrounding the ejaculatory duct playing a part as in *C. zealandica* and Bordas (1900) makes no mention of such a sheath in two Lucanidae. A muscular sheath enclosing fluid is, however, present around the ejaculatory ducts of the melolonthines *M. melolontha* (Straus-Dürckheim 1828) and *P. anxia* (Berberet & Helms 1972) and in the scarabaeine *Coprophanaeus lancifer* (Edmonds 1974). Berberet & Helms (1972) called it the "erection fluid pump" and report that fluid within it causes the internal sac to enter the bursa copulatrix. Edmonds (1974) suggested that the fluid within it also played a part in everting the internal sac in *C. lancifer*. It appears likely that a similar mechanism applies to *M. melolontha* although the penis sclerites fuse to form a ventral strut in this beetle (Straus-Dürckheim 1828) and the function of this is not clear.

Berberet & Helms (1972) and Rittershaus (1927) provided some information on the mechanics of copulation of *P. anxia* and of two rutelines.

Muscle number	<i>Phyllopertha horticola</i> L. (Rutelinae) Rittershaus (1927)	<i>Anomala ausonia</i> Erichs. (Rutelinae) Lupo (1947)	<i>Coprophaneus laticifer</i> (L.) (Scarabaeinae) Edmonds (1974)	<i>Geotrupes stercorosus</i> Scriba (Geotrupidae) Hieke (1966)
Extrinsic muscles of the aedeagus				
1	Die Protraktoren der Rutenkapsel	Muscolo estensore dell'organo copulatore	...	M. tergoapodemo-phallobaso-apodemalis medialis
2	M. tergoapodemo-phallobasoapodemalis lateralis
3	muscle e	M. paratergo-phallicus
4	muscle b	M. antecosta-antecostalis urosterni VIII
5	muscle a	—
6	[muscle d]	M. antecosta-antecostalis uronotum lateralis VIII
7	[muscle c]	—
8	—
-	M. phallobasicus externus
-	M. phallobasoapodemalis
Intrinsic muscles of the aedeagus				
9	(Der zweite Muskel der Ventralplatte) (Der paarige Attraktor der Ventral platte)	[Muscoli attrattori anteriori della piastra ventrale] [Muscoli attrattori laterali della piastra ventrale]	...	M. phallobasoapodemo-phallobasicus medialis
10	—	—	...	[M. phallobasoapodemo-phallobasicus]
11	Die Protraktoren des Penis	Muscoli protrattori del pene	...	M. phallobasoapodemo-phallobasicus superior
			...	M. phallobaso-phalloapodemalis
			...	[M. phallobasoapodemo-phalloapodemalis superior]
			...	[M. phallobasoapodemo-phalloapodemalis basalis]
			...	[M. phallobasoapodemo-phalloapodemalis inferior]
			...	[M. phallobaso-phallicus]
12	Die Retraktoren des Median Lobe	Muscoli retrattori del pene	...	M. phallo-ductalis
13	Die Retraktoren des Inneren Sackes	Muscoli retrattori del sacco prepuziale	...	M. endophallicus.
14	...	Muscolo costrittore distale del canale eiaculatore	...	M. phallobasicus internus
15	—

respectively. Their accounts of tegmen movements are almost identical with those in *C. zealandica* with the exceptions that in these rutelines the parameres are fused to the basal piece and the basal piece has only one pair of extrinsic muscles (Table 2, 3). The latter originate on the spicules and insert on the second connecting membrane near the right of the tegmen so they are responsible for both rotating and extending the tegmen. The anatomical descriptions of Straus-Dürckheim (1828) and Hieke (1966) also suggest that the tegmens of *M. melolontha* and *G. stercorosus*, respectively are protracted and retracted in much the same way as in *C. zealandica*. The only apparent difference is that the parameres of *M. melolontha* move together to clasp within the female (Rittershaus 1927) and no evidence of this was found in *C. zealandica*.

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Lipid composition of a clutch of kakapo (*Strigops habroptilus*) Aves: Cacatuidae) eggs

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Abstract The lipid compositions from yolks of a clutch of four infertile kakapo eggs were determined and compared with those of other species. The principal components were triacylglycerols (64%) and phospholipids (23%), made up mainly of phosphatidyl choline (16%) and phosphatidyl ethanolamine (3%). Studies of the individual fatty acid compositions of these lipids were undertaken and the stereospecific distribution of the saturated and polyunsaturated essential fatty acids in the major phospholipids reported. These results, together with those for the fatty acid compositions of lipids extracted from the dietary intake of plant material available for the kakapo, indicated that there is adequate linoleic acid in the birds' diet. Also, no toxic fatty acids occurred.

Keywords *Strigops habroptilus*; kakapo eggs; lipids; fatty acids; stereospecific distribution; nutritional requirements

INTRODUCTION

The kakapo is a flightless, nocturnal parrot, endemic to New Zealand. Although formerly widespread over the three main islands of New Zealand (Williams 1956; Dawson 1962; Millener 1981), only four small kakapo populations remain today. Two are naturally occurring populations: one, consisting now only of males, has a fragmented distribution in Fiordland; the other is a breeding population in southern Stewart Island, from which 25 birds (5 females and 20 males) have been extracted and transferred to predator-free Codfish Island. Less than five birds probably remain on Stewart Island (R. G. Powlesland, unpubl. data). Two further populations are being established on offshore islands free of introduced mammals, except Kioie (*Rattus exulans*). In 1982, 22 kakapo (9 females and 13 males) were transferred to Little Barrier Island, where at least 14 were alive at August 1986 (C. R. Veitch, pers. comm.). Thus, the kakapo is currently one of the world's rarest species, its total population probably numbering less than 50 birds. No kakapo are in captivity.

The eggs of other endangered species such as the little spotted kiwi (*Apteryx oweni*) (Body & Reid 1987) or takahe (*Notornis mantelli*) (Body 1984) have been investigated by comparing the fatty acid compositions of their infertile yolk lipids with the level of essential dietary fatty acids provided. Low quantities of essential fatty acids, particularly linoleic acid (18:2) in the egg yolk, reflect the low dietary intake that can seriously affect the survival of chicks (Menge 1968; Body & Reid 1983). Now that most kakapo have been transferred to safer locations to reduce introduced predator hazards, similar information on the lipid composition of their infertile egg yolks and natural diet could determine whether lipid deficiencies may be a problem for the kakapo.

In this paper the fatty acid composition of both a mixture of plant material eaten by kakapo and the individual lipid classes of the eggs were compared. We attempted to determine whether adequate levels of essential fatty acids were available in the diet and

eggs for normal chick development, and to detect the presence of undesirable dietary fatty acids in the kakapo's diet, such as erucic or cyclopropene fatty acids, that could affect detrimentally the health of chicks (Donaldson 1967; Pearson et al. 1972; Vogtmann et al. 1974). This information on lipid composition and quantity of kakapo food and eggs from Stewart Island may be useful in future efforts to conserve the species through supplementary feeding.

METHODS

Eggs

A complete clutch of four kakapo eggs from southern Stewart Island (167°46'E 49°09'S) was available for investigation. The clutch, laid in late January 1985, was removed from the nest on 16 March 1985, when it was evident they would not hatch. Incubation of fertile eggs is estimated to take about 25 days (R. G. Powlesland, unpubl. data).

Foods

Kakapo are herbivores, the diet made up of a wide variety of species ranging from small plants to tall forest trees (Best 1984). Two mixed groups of plant materials were selected for investigation.

Plant mix 1: A mixture of common forest foliage eaten throughout the year including *Cyathodes juniperina* fruit, *Korthalsella salicorniodes* plants, *Thelymitra venosa* plants, *Blechnum* spp. rhizomes and leaves, *Olearia colensoi* leaves, *Lycopodium ramulosum* rhizomes, *Dracophyllum longifolium* leaves, and *Gahnia procera* leaf bases. Although any order of preference or quantities consumed by

the kakapo in the wild could not be accounted for, a representative aliquot (approximately 200 mg each) of the plant species listed above were combined together and classified as the "basic" diet of kakapo.

Plant mix 2: A mixture of yellow-silver pine (*Halocarpus biformis*) pollen cones and fruit, which is eaten during the breeding period.

These diets were freeze-dried, finely ground, and refrigerated for storage.

Lipid extraction

The plant mixes were homogenised and extracted with CHCl_3 -MeOH (2:1 v/v) as described by Folch et al. (1957) and the recovered lipid extracts were weighed. The total contents from all eggs were carefully forced through a small hole (1 cm diameter) drilled into the intact egg shells following the application of a slight internal pressure of nitrogen (Body 1984). The contents of eggs 1 and 2 were separated into their individual yolk and albumen groups. These fractions were freeze-dried and their dry matter contents were determined.

The contents from eggs 3 and 4 were homogenised independently and extracted with CHCl_3 -MeOH (2:1 v/v) as outlined above. This separated the egg lipid extracts suitable for analysis from their corresponding crude protein residues.

Lipid analysis

The lipid extracts (400–500 mg) from each of eggs 3 and 4 were fractionated into their respective neutral and polar lipid classes by silicic acid column (40 g) chromatography, with both CHCl_3 and MeOH as the eluting solvents (Body & Reid 1983). The polar

Table 1 The general characteristics of kakapo eggs.

	Egg 1	Egg 2	Egg 3	Egg 4
Dimensions (mm)	51.8 × 37.7	50.8 × 40.0	50.5 × 37.8	50.5 × 37.5
Total weight (g)	33.73	32.60	32.91	30.90
Shell (g)	3.27	3.23	2.90	2.80
Lipid extract (g)*	—	—	0.50	0.57
Protein residue (g)*	—	—	1.36	1.54
Lipid:protein	—	—	1:2.72	1:2.70
Albumen (g)†(% water)	16.54 (83.72)	18.17 (89.40)	—	—
Yolk (g)†(% water)	10.74 (62.26)	10.01 (59.07)	—	—
Yolk:albumen	1:1.54	1:1.82	—	—

*Related to quantity of total egg contents taken for lipid extraction.

†Egg contents subdivided into two main groups.

ds from both eggs were combined (about 160) and rechromatographed on another silicic acid mnn (40 g) and resolved by eluting with CHCl₃-OH solvent mixtures of increasing polarity ngth. Details have been described by (Body 5).

Gas chromatographic procedures used to rmine the fatty acid composition of the diets and individual lipid classes of the egg yolks have n reported fully (Body 1984). Details of the eoespecific distribution of the individual fatty ls amongst the sn-1 and sn-2 sites of the principal sphatidylethanolamine and phosphatidyl choline ar lipids were obtained by the application of ctive phospholipase-A2 hydrolysis with snake om (*Crotalus adamanteus*, Ross Allan Reptile titute, Silver Springs, FL, USA) (Long & Penny 17; Lands & Hart 1964) and resolving their rolysis products by thin-layer and gas omatography (Body & Newman 1989).

RESULTS AND DISCUSSION

e general characteristics of the clutch of kakapo s are shown in Table 1. The weights of these eggs re within the range of 30.9–33.7 g and the e responding dry egg shells amounted to between –9.9% of the total mass. It was noted the yolk/ umen ratios for eggs 1 and 2 are similar to the k/albumen index given by Ricklefs (1977) for the s of precocial species (0.64), rather than that for icial species (0.28). However, since the eggs re analysed after a protracted incubation period lagainst the increasing natural loss of the original ter content, these figures should be used as a de only. Nevertheless, this time lapse did not ose any degradation of their lipid content because substantial level of hydrolysed fatty acids was served during the related analytical processes.

The lipid composition of the kakapo eggs 3 and Table 2) shows that the general distribution of the in lipid classes was in the range of 74–79% utral and 21–26% polar lipids. This pattern is

similar to that for other bird species, e.g., domestic hen (*Gallus domesticus*) 70% and 30% (Body & Reid 1983) and takahe (*Notornis mantelli*) 72–74% and 26–28%, respectively (Body 1984). The detailed phospholipid composition (Table 3) follows a pattern similar to that for other birds, i.e., phosphatidyl choline (70%) and phosphatidylethanolamine (11%) (Rhodes & Lea 1957; Privett et al. 1962). However, the rather high (13%) level of the fraction labelled cardioliipin also included other unidentified components that were eluted from the column with similar chromatographic properties.

The fatty acid composition of the kakapo's diet can be compared with that in the egg yolk (Table 4). The dry matter of both plant mixes (1 and 2) had similar, small quantities of extractable oil, namely 3.5 and 3.4%, respectively, but their fatty acid composition differed (Table 4). Plant mix 1, being predominantly foliage, provided lipid extracts with higher levels of linoleic (18:2) and linolenic (18:3) acids than plant mix 2. In addition, plant mix 2 had greater quantities of both oleic (18:1) and long-chain saturated (20:0, 22:0, and 24:0) fatty acids than the other dietary source. These latter fatty acids were not substantially observed in the egg yolk lipids (Table 4) probably because they cannot readily be absorbed from the maternal gut, as has been demonstrated with other animals (Body & Hansen 1978; Body & Grace 1983).

Compared with the minimal requirements of 2% 18:2 fatty acids in the dietary intake needed by domestic hens to breed healthy chicks (Menge 1968), the quantity of 18:2 fatty acid in the kakapo's freeze-dried dietary mixture examined appears lower (about 0.5%). It is always difficult to estimate the quantities of foliage consumed each day by "grazing" birds in the wild, e.g., takahe (Body 1984). However, provided substantial food is present even with low levels of lipid extract from the leaves and stems rich in 18:2 or 18:3, if an adequate volume of foliage is consumed, satisfactory quantities of essential fatty acids will be available.

ble 2 The lipid composition of kakapo eggs, expressed weight percentage of total lipid extracts.

Components	Egg 3	Egg 4
olesteryl esters	3.9	2.0
acylglycerols	60.5	67.5
olestrol + fatty acids	9.9	9.8
ospholipids	25.7	20.7

Table 3 The phospholipid composition of kakapo eggs, expressed as weight percentage of combined phospholipids.

Components	%
Cardioliipin	13.0
Phosphatidyl ethanolamine	10.8
Phosphatidyl serine, Phosphatidyl inositol	3.2
Phosphatidyl choline	70.2
Sphingomyelin	2.8

The direct effect that dietary fatty acids have on the fatty acid content of the egg yolk was demonstrated when domestic hens were fed diets including (i) fish meal (Edwards & Marion 1963; Navorro et al. 1972), (ii) rapeseed oil (Vogtmann et al. 1974; Vogtmann & Clandinin 1975), or (iii) cottonseed oil (Phelps et al. 1965; Abou-Ashour & Edwards 1970). The egg yolk fatty acids of these hens were enriched with either (i) W3-poly-unsaturated, (ii) erucic (22:1 W9), or (iii) cyclo-propene fatty acids. The latter two acids are relatively common in some plant oils and it is important to make sure they are absent from the diet. Their presence can be reflected by the reduced $\Delta 9$ -desaturase activity with saturated fatty acids in the hen's liver, which explains why such diets are not successful in breeding healthy chicks (Donaldson 1967; Pearson et al. 1972; Vogtmann et al. 1974). Neither of these undesirable fatty acids were detected in the kakapo diets so they cannot be involved in reducing the survival of the kakapo in their natural habitat.

The fatty acid pattern in the individual lipid classes of the kakapo egg yolk can be related to the dietary resources available. In particular, the proportions of either 20:4 W6 or 22:6 W3 biosynthetic products in each lipid fraction can be related to the required dietary levels of their respective precursors (18:2 W6 and 18:3 W3). These polyunsaturated fatty acids are bound principally to the sn-2 position of the glycerol moiety of both the phosphatidyl ethanolamine and phosphatidyl choline fractions and balanced with the saturated fatty acids at the sn-1 sites. These features have been reported in the phospholipid fatty acid studies of other bird egg yolks (Hawke 1959; Privett et al. 1962).

When these fatty acid calculations are amended to the total egg contents and expressed as mg g⁻¹ lipid extracts, these can be more directly compared with those of the domestic hen (Table 5). It can be assumed that any quantities of essential fatty acids above those recommended by the poultry industry (Menge 1968; Balnave & Weatherup 1974) for

Table 4 The fatty acid composition of the diets and individual lipid classes of kakapo eggs. This includes stereospecific distribution of fatty acids in the main phospholipid fractions. All results are expressed as percentage by weight of the total fatty acids (tr, <0.1%; -, not detected; Wno, the carbon atom numbered from the terminal methyl group at which the double bonds commence; Diet 1, mixture common kakapo food; Diet 2, yellow-silver pine pollen cones and fruit).

Designation*	Diet 1	Diet 2	Triacylglycerol	Cardiolipin	Phosphatidyl ethanolamine		Phosphatidyl choline	
					sn-1	sn-2	sn-1	sn-2
n-Saturated								
14:0	0.7	0.7	0.3	0.7	0.1	0.7	0.6	0.1
15:0	—	—	0.1	0.2	tr	0.2	0.2	tr
16:0	29.7	29.6	16.3	16.5	6.5	1.5	24.9	1.3
17:0	—	—	0.4	0.3	0.1	0.2	0.3	tr
18:0	4.0	2.0	11.4	24.4	36.5	2.0	16.4	0.2
20:0	3.8	7.6	0.1	0.2	0.1	tr	tr	0.1
22:0	0.9	11.0	—	—	—	—	—	—
24:0	2.0	4.3	—	—	—	—	—	—
n-Unsaturated								
14:1 W5	—	—	tr	0.2	0.1	0.3	0.2	tr
15:0 W6	—	—	tr	1.9	1.8	1.3	0.2	tr
16:1 W7	tr	1.1	2.3	0.9	0.1	0.7	0.7	0.2
17:1 W8	—	—	0.1	4.3	3.3	1.4	0.1	tr
18:1 W9	10.4	17.7	51.7	18.7	0.2	14.1	3.5	13.6
18:2 W6	28.0	17.1	11.9	9.0	0.1	12.3	0.9	10.6
18:3 W3	20.5	8.9	4.8	2.1	0.4	1.4	0.5	0.5
20:2 W9	—	—	—	0.1	0.1	0.4	—	0.1
20:3 W9	—	—	—	1.2	—	2.5	—	3.5
20:4 W6	—	—	0.3	11.0	0.5	7.1	1.0	15.4
20:5 W3	—	—	0.3	1.3	0.1	0.7	0.5	1.4
22:4 W6	—	—	—	1.3	tr	0.7	—	0.5
22:5 W3	—	—	—	1.2	tr	0.8	—	0.5
22:6 W3	—	—	—	4.5	tr	1.7	—	2.0

*Carbon number: number of double bonds.

able 5 The distribution of major fatty acids within the pids of kakapo and domestic hen eggs, expressed as mg -1 lipid extract.

		Fatty acids					
pecies		16:0	18:0	18:1	18:2	20:4	22:6
akapo	Egg 3	146.7	106.9	319.1	86.8	29.0	4.9
	Egg 4	143.7	98.8	353.4	92.6	24.7	6.0
omestic Hen		235.7	84.2	370.1	67.3	11.8	3.4

ccessful hatchings would be beneficial for other pecies. These observations (Table 5) clearly show e kakapo egg yolk contains adequate amounts of 8:2 and 20:4 which confirms that the Stewart Island akapo's dietary intake was satisfactory. It can be oncluded if these eggs were fertile, the survival rate f hatched kakapo chicks would not have been inhibited by their egg's lipid content.

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A review and revision of the genus *Rhyphodes* Stål (Hemiptera: Lygaeidae)

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Abstract New Zealand now has more species of Orsillinae than any continent, being second only to the Hawaiian Islands in proliferation of species. Twenty-two new species of *Rhyphodes* Stål: *argenteus*, *atricornis*, *brachypterus*, *brevifissus*, *brevipilis*, *bucculentus*, *celmisiae*, *cognatus*, *crinitus*, *leptilis*, *eminens*, *gracilis*, *hirsutus*, *jugatus*, *koebelei*, *longiceps*, *longirostris*, *rupestris*, *russatus*, *spadix*, *townsendi*, and *triangulus* are described and figured. *Hudsona* Evans 1929 is synonymised with *Rhyphodes*. The six previously known species are redescribed and figured. Limits of the genus are set and a key to distinguish the 28 species now known in *Rhyphodes* (which is endemic to New Zealand) is provided. A lectotype has been designated for *Nysius zealandicus* Dallas. There is an illustrated general morphology section and a list of taxonomic characters. The results of a numerical phenetic analysis using 96 characters is presented. Some abnormalities in venation on the forewing membrane and on the hindwing are described and figured. Toothed spines on the abdominal membrane near the inner laterotergites are described. There is a progression of siting of abdominal spiracle VII from a central position to the lateral edge of the dorsal connexivum surface. Biological information on host plants and habitat are given, as are distribution maps of the eight most abundant species. A possible zonation on one mountain as a result of competition between species is suggested.

Keywords Systematics; taxonomy; Hemiptera; Lygaeidae; Orsillinae; tribes; *Rhyphodes*; *Hudsona*; new species

INTRODUCTION

Rhyphodes clavicornis (Fabricius, 1794) from New Zealand was the first species of Orsillinae in the world to be described. At the time of writing, the genus *Rhyphodes* Stål 1868 (which is endemic to New Zealand) contained five species: *clavicornis* plus four species described by Usinger (1942b) namely, *chinai*, *myersi*, *sericatus*, and *stewartensis*. *Nysius anceps* White 1878 assigned to the new genus *Hudsona* by Evans (1929a), is herein included in *Rhyphodes*.

After completing his specialist study on the Hawaiian Orsillinae (Usinger 1942a) and studying the few specimens and species then available from New Zealand, Usinger (1942b) commented on their remarkable diversity, grouping New Zealand with Hawaii and the Galapagos for the most unique forms of Orsillinae.

I have had an ongoing interest in the Orsillinae of New Zealand for most of my working life, beginning with a Masterate thesis on *Nysius huttoni* (White, 1878). From collecting trips it soon became apparent that there are many remarkable new species. I collected many of them over some 12 to 14 years, particularly between 1962 and 1973 inclusive, from remote alpine areas with my colleague Mr Ian Townsend.

When my friend the late Professor P. D. Ashlock, who wrote a generic classification of the Orsillinae of the world (Ashlock 1967), saw some of these new forms from New Zealand, he commented that it was one of the more incredible boxes of Orsillinae he had ever seen.

As so little material and only a handful of species had been collected, it was not possible for previous workers to adequately describe the genus *Rhyphodes* or to define its limits.

The present work aims to redescribe the genus *Rhyphodes*, define its limits, and describe the 28 species now known to belong to it. Twenty-two new species are described. A key to species, and results of a numerical phenetic analysis in the form of phenograms and a three-dimensional ordination graph are presented, but no phylogenetic speculation is attempted. Biological notes on host plants and

habitat are given. An introductory section on general morphology is included, in which the most useful characters for recognition of species are indicated.

In attempting to solve one or two problems some mistakes may have been made; it is hoped that these are minimal. Three main areas for further work have come to light. One, to determine if *R. myersi* is limited in distribution on Coronet Peak by competition from other species. Two, to determine if *cognatus* n. sp. is distinct from *clavicornis*, and if not, what causes lack of pronotal triangles in all but a few specimens of *clavicornis* in the South Island. Three, to determine whether *chinai* contains more than one species as some specimens appear to vary in width and colour and some lack pronotal triangles. Further, the species from the Three Kings Islands (Woodward 1954) was not included in the present study so its status has yet to be established.

GENERAL MORPHOLOGY

Most of the structural terms used in the descriptions are illustrated in Fig. 1–6. The general appearance from the dorsal aspect is shown in Fig. 1, whilst Fig. 2 shows the insect in lateral view.

The head is of the usual Lygaeoid form (Spooner 1938), is correct, has prominent ocelli on the vertex, and large bucculae. In side view, the head varies in shape from relatively long and thin (Fig. 100, 146) to short and thick (Fig. 2, 175). The portion between anterior of eye and antennal tubercle is variously declivous.

Pronotum broad at posterior, sides straight or sinuate (Fig. 1), disc slightly convex, rarely flat, but may be elevated posteriorly with sides flaring to posterior (Fig. 142). Punctuation dense or widely spaced (Fig. 166), coarse or shallow. Scutellum with tri-radiate ridge. Apex may be acute or rounded, upturned or level.

The hemelytra consisting of clavus, corium, and membrane (Fig. 7) show the general pattern of venation described in the Orsillinae by Ashlock (1967). The same terminology is followed here. On the corium Sc is separate, basally running alongside, perhaps slightly below, R+M (viewed from underneath and from side). In some species there is a row of punctures between Sc and R+M in basal half.

One notable deviation from the general pattern is the curving and joining of 1A to PCu on the membrane (Fig. 8) in *celmistiae* n. sp., *crinitus* n. sp., *gracilis* n. sp., *russatus* n. sp., and in females (except one) but not all males of *atricornis* n. sp.

Where Cu forks, the angled portions (like crossveins) at the start of each fork are usually even. In some species the angled portion of PCu is longer, in others that on Cu is longer. In *eminens* n. sp., Cu usually comes straight down from the common stem. In *bucculentus* n. sp. the common stem is curved, not straight.

An interesting phenomenon noted in six species (although it cannot be used in classification) is a change in, or addition to, the venational pattern on the forewing membrane on one wing only, and in only one specimen of a species (Fig. 9–18).

The hindwing venation is of the generalised (least specialised) orsilline pattern as described by Slater & Hurlbutt (1957) in that the intervinals or secondary veins (SV) and jugal vein (2A) are present, the secondary veins fused basally (Fig. 19). M and Cu are "joined" for a short distance as in most orsilline genera (Ashlock 1967). In addition, Sc is present on and supporting the leading edge in the apical half (Fig. 19) and is combined with R in the basal half. It occurs in other Lygaeidae, namely *Oncopeltus* Stål 1868 and *Lygaea* Fabricius 1794 (in both of which it is separate from base and continues in apical half) and *Dieuches* Dohrn 1860. In one undetermined mirid (Mirini) Sc+R divides into two tubular branches for a short distance, Sc then continuing on the leading edge. Sc probably occurs throughout the Lygaeidae and Miridae because the leading edge of such a delicate wing would need support in the apical half. Confirmation is given by Sweet (1967) and Malipatil (1978) who record and figure Sc in the same place on the hindwing of the cleridine complex and the Myodochini, respectively (Rhyparochrominae: Lygaeidae). Slater (1982) also states that Sc is indistinct and marginal in the Miridae.

A short stump of a branch on Cu (Fig. 20) was found in the new species *R. rupestris*, *eminens*, *gracilis*, and *koebelei*. In females (except *eminens*) it reached the anterior vanal fold, in males (and female *eminens*) it was only half that length. In some specimens of both sexes it was less clear, appearing as a posteriorly directed kink in the posterior margin of Cu at that point. A similar kink on Cu (although no branch) was noted in some specimens of *brevifissas* n. sp. (Fig. 21), *chinai*, and *spadix* n. sp.

Such a stump branch on Cu and also on M was noted by Slater & Hurlbutt (1957) in *Eremocoris fesus* (Say, 1931) (Rhyparochrominae, tribe Drymini). It is rather unusual as this was the only occurrence in 83 species of Lygaeidae they examined. It is not present in the type species of any of the orsilline genera (Ashlock 1967).

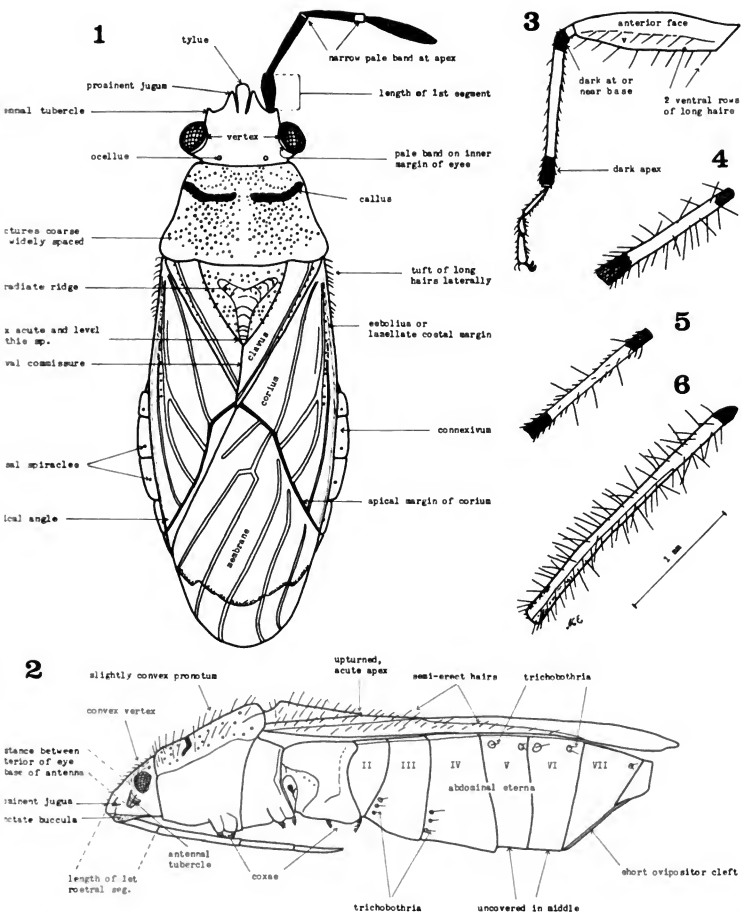


fig. 1-6 Illustrating structural terms. 1, on a dorsal view outline of *Rhypes townsendi* n. sp. holotype ♀; 2, as seen lateral view on a paratype ♀ of *R. jugatus* n. sp. (Mt Domett); 3, on right foreleg of *R. stewartensis* ♂ from Manapouri = ventral surface); 4, left fore tibia, dorsal aspect of *R. spadix* n. sp. paratype ♀; 5, mid tibia of same, dorsal aspect; 6, left hind tibia of *R. hirsutus* n. sp. paratype ♀ (Kaweka Range). Scale is for Fig. 3-6.

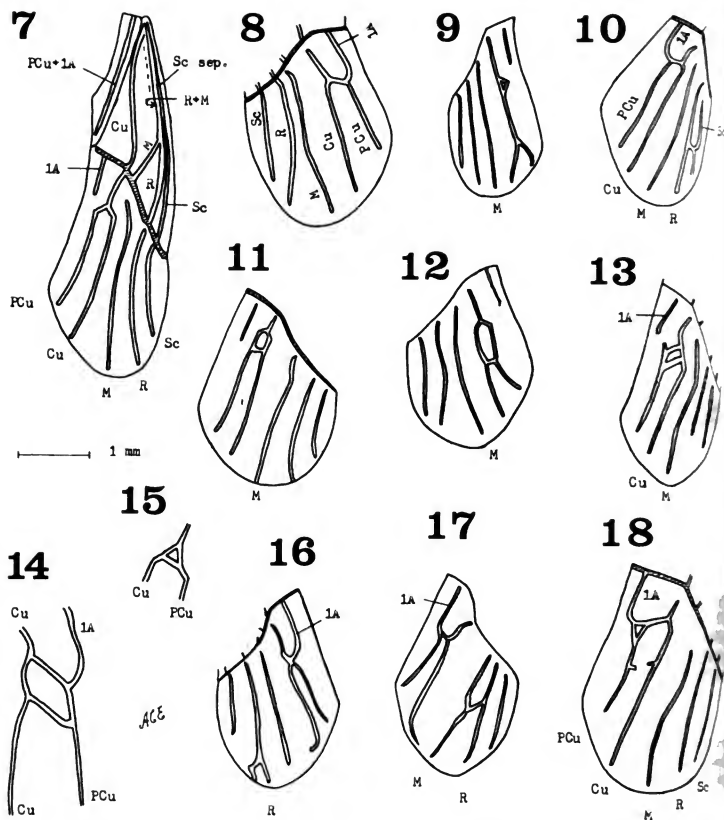
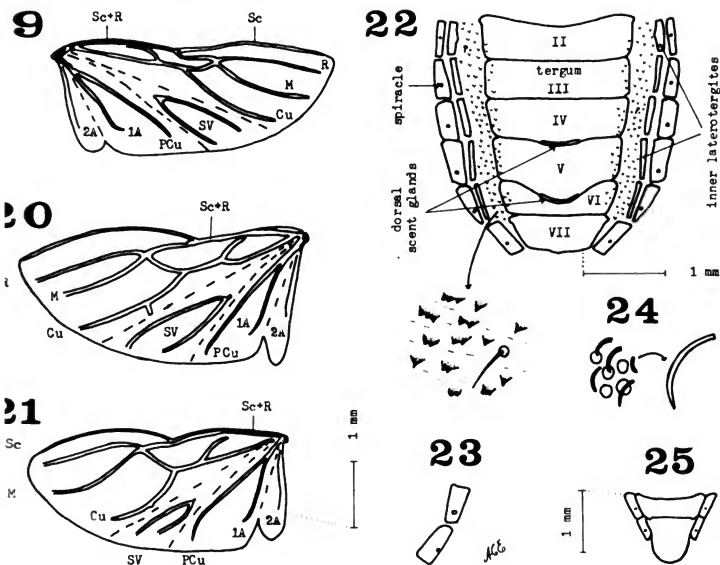


Fig. 7-18 Wing venation. 7, Right hemelytron of *R. clavicornis* ♂ (Rimutakas); 8-18 membranes of: 8, *R. celmis* n. sp. paratype ♀ (Coronet Peak), left membrane; 9, *R. rupestris* n. sp. paratype ♂, left membrane; 10, *R. gracilis* n. sp. paratype ♂ (Mt Sebastopol), right membrane; 11, *R. brevipilis* n. sp. paratype ♂, right membrane; 12, *R. rupestris* paratype ♀, left membrane; 13, *R. gracilis* paratype ♀ (Mt Sebastopol), right membrane; 14, *R. bucculentus* n. sp. paratype ♀, part left membrane; 15, *R. bucculentus* paratype ♀, part left membrane (both Wairau Bridge); 16 (left), 17 (right) membrane of *R. emimens* n. sp. paratype ♀; 18, *R. atricornis* n. sp. paratype ♀ (Wilmot Pass), right membrane.



19–25. 19–21 Hind wing venation of: 19, *R. clavicornis* ♂ (Rimutakas); 20, *R. rupestris* n. sp. paratype ♀; 21, *R. brevifissus* n. sp. paratype ♂ (Ohakune) (dashed lines = folds); 22, dorsal abdominal surface of *R. clavicornis* ♀ (Rimutakas); 23, connexivum VI and VII of *R. atricornis* n. sp. paratype ♀; 24, pubescence on *R. clavicornis* in relation to notal punctures (♂ Rimutakas); 25, tergum and connexivum of abdominal segments VI and VII of *R. brachypterus* n. sp. paratype ♂.

One problem encountered with hindwing venation is the imprinting of vein pattern of the hindwing above or below, and sometimes of part of forewing membrane veins, because of the pressure of wings on one another and the top of the forewing membrane veins. It is therefore necessary to be aware of the position and slant of veins of the opposite wing and the hemelytra membrane above. On two species was at first thought that 2A was branched, but one turned out to be an imprint of 1A, because the anal lobe is folded under. Where 1A curved toward the apex, the imprint curved away in the opposite direction like a mirror image when the anal lobe was folded.

Legs with characters as in Fig. 3–6. Femora not swollen (except moderately in *anceps* and

brachypterus n. sp.), but slender in two species. Femora unarmed, but with two rows of long hairs ventrally (rarely on fore femora only) and often with other erect or semi-erect hairs or short hairs. Tibiae usually with short hairs (Fig. 3). Fore tibia often with long outstanding hairs, longer than width of tibia at middle (Fig. 4) or with a mixture of long and short hairs. Mid tibia sometimes, hind tibia rarely, with a few outstanding hairs in addition to short hairs (Fig. 5). Rarely all tibiae covered with long outstanding hairs (Fig. 6). Tibiae usually dark at apex and base or near base.

The abdomen (Fig. 2, 22) possesses two dorsal scent glands between segments IV and V, V and VI in both adults and nymphs (Usinger 1938, 1942a; Putshkov 1958; Scudder 1963; Ashlock 1967), and

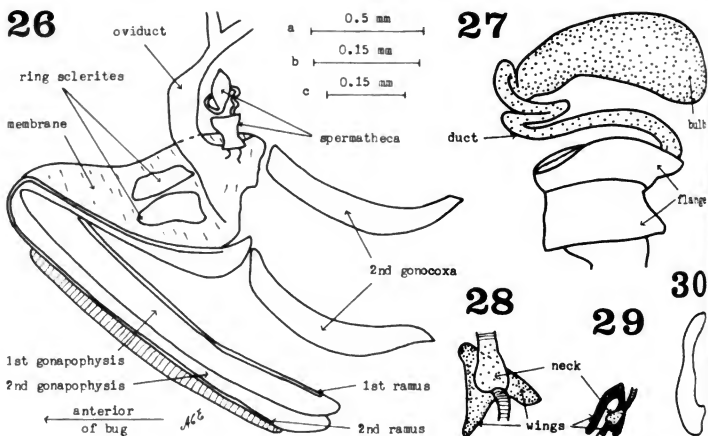


Fig. 26-30. Genitalia. 26, Female genitalia of *Rhyphodes* drawn from paratype of *R. emimens* n. sp.; 27, spermatheca of *R. clavicornis* (♀ Rimutakas); 28, ejaculatory reservoir of *R. clavicornis* (♂ Coromandel); 29-30 *R. sericatus* (♂ Kaikouras); 29, ejaculatory reservoir; 30, left paramere. Fig. 26, 30 to scale a; 29 to twice scale a; 27 to scale b; 28 to scale c.

inner laterotergites between the connexivum and terga (Ashlock 1967). All abdominal spiracles, II-VII, are dorsal (Putshkov 1958; Scudder 1963; Ashlock 1967). The last abdominal spiracle (segment VII) in *R. atricornis* n. sp. is right on the lateral edge (Fig. 23), whereas in other species it is in a more central position (Fig. 22). Trichobothria having the typical lygaeid arrangement (Scudder 1963). All ventral abdominal sutures are straight and all reach the lateral margin (Putshkov 1958; Scudder 1963; Ashlock 1967).

In *Rhyphodes* a new discovery is the presence of tiny sclerotised, tooth-like spines on the membrane between the terga and the inner laterotergites (Fig. 22). These often occur on the edge of the terga and in one or two species right across the terga. The occasional bristle-like spine also occurs on the membrane.

Although spiracles II-VI are on the centre line of the connexivum, in *Rhyphodes* we see a progression in the placement of spiracle VII from the outer third to the outer quarter to the outer sixth (three species) to right on the lateral edge. In the Australian

Lepionysiini Ashlock 1967 spiracle VII is ventral. Are we seeing in *Rhyphodes* a movement which in the future may see spiracle VII appear on the lateral edge on the ventral surface in one or more species? It was also noted that the spiracle opening of those close to the edge pointed posteriorly, not dorsally. The ventral position of spiracle VII in *Lepionysiini* Ashlock 1967 may not yet have stabilised, however, as Slater (1976) showed that its position is variable between both sides dorsal and both ventral. Most specimens had both exactly laterally, although some had one either dorsal or ventral and the other lateral.

Hairiness. All species have pubescence. Most species have white, ordinary, sickle-shaped, appressed pubescence (Fig. 24), sparse in one species. Two species have very short pubescence and one species has long, dense pubescence.

All species have erect hairs on the anterior pronotal lobe. Most species have erect or semi-erect hairs on the dorsum of the head, posterior pronotal lobe, and scutellum (Fig. 2), and a tuft of long hairs laterally at base of costal margin (Fig. 1), but four or five species lack hairs in these locations. In addition,

These species have semi-erect hairs on the hemelytra, well distributed or near base of clavus and on the abdomen only, whilst in other species they are absent. Usually, three species are covered with long standing hairs.

Chromosomes. The behaviour and size of the chromosomes during meiosis has been described for *R. clivicornis*, *R. anceps*, and *R. myersi*, and figured for the first two species by Ueshima & Ashlock (1980). For *R. clivicornis* they report the diploid number of chromosomes as $14 (12 + XY)$ and the haploid number as $5 + m + XY$.

Male genitalia

The male genitalia (Fig. 26) are of the usual scissor-like form, blade-like and exerted (Scudder 1959), the terminology adopted is that of Scudder (1959). Ring sclerites are present on the roof of the genital capsule but their borders are plain, lacking sclerotised and spined basal border noted in *Rhypharochrominae* (by Eyles (1973). In *R. clivicornis* there was a hint of a fold at the base, where the border was slightly thicker and darker with a wavy outline (Fig. 50). Spermatheca (Fig. 27) with blade either elongate or round, duct usually short, apically turned back on itself once or twice, then following rim of flange in a sweeping curve (Fig. 80), but sometimes long and disorganised (Fig. 116) with characteristic flange (Ashlock 1967; Eyles & Ashlock 1969). The upper lip of the flange, though usually angled outwards, may be broad and flat at a right angle (Fig. 163), or rolled (Fig. 156).

Female genitalia

The aedeagus of *R. clivicornis* has been figured and described by Ashlock (1967) in a general description of the Nysini aedeagus, and is clearly of the form described in other Orsillinae (Ashlock 1957, 1967). The terminology follows that of Ashlock (1957) but uses the term 'ring sclerite' which he abandons in his 1967 work. From a knowledge of the many species herein described, the aedeagus of *Rhypodes* may be characterised as follows:

Basally there is a short sclerotised or partly sclerotised phallosome, from which the more distal parts are exerted. The conjunctiva is long and entirely membranous, with a sclerotised band apically (Fig. 31). Although many species lack conjunctival lobes, a handful of species have one or two, membranous lobe proximal to the sclerotised band (Fig. 159) and another one or two species have no such lobes (Fig. 63, 130).

The vesica (which is all that part distal to the base of the ejaculatory reservoir) has two large, ear-like lobes (Fig. 31); the first is sclerotised, the second is sclerotised underneath on its base. There follows another large membranous lobe and one or more smaller membranous lobes. Some species have a small membranous lobe before the ear-like lobes (Fig. 31, 110). There is no gonoporal process or free part of the seminal duct, which ends at the inflatable apex of the vesica. The secondary gonopore is distinctly flared (Fig. 96).

The ejaculatory reservoir (Fig. 28) is quite large, with a large bulbous neck and wings which are often broad, flat and triangular, or A-shaped (Fig. 29). The body and wings have fused, so there appears to be no body. Ashlock (1957) stated that "all of these structures may undergo fusion or reduction." On the orsillines he stated that there is a strong tendency for reduction of the ejaculatory reservoir in this group, and in *Nysius californicus* Stål 1859, among other reductions, stated "body lost."

Left and right parameres are mirror images of one another. Most species have the blade short, curved and tapering throughout (Fig. 95, 109). In some species the blade is long, straight for part of its length and not tapering, giving a broad, flat appearance (Fig. 30, 106).

Where aedeagus reaches in copulation

During copulation the ovipositor is not straightened out as for oviposition. The distal section is merely lowered from the ovipositor cleft and there is still an acute-angled bend. As the aedeagus has to get round this bend, it is theorised that the tip of the ovipositor must be locked into position hard against the phallosome before the aedeagus begins to inflate, and that the vesica does not inflate until the conjunctiva reaches the bend.

The fully inflated aedeagus has a bend at the ejaculatory reservoir (Fig. 31) and from dissection of pairs in copulation it is confirmed that the bend at this place in the aedeagus lies in the bend in the ovipositor.

The function of the inflatable lobes on the vesica is to lift the upper membrane (or part the upper and lower membranes) in the female genital capsule so that the secondary gonopore and end of the seminal duct can be inserted into the short spermathecal duct below the flange at the base of the spermatheca (Fig. 54). The female membranes must be slack to permit this. The terminal big lobe on the vesica juts forward beyond the end of the seminal duct (pushing the female membrane into the shape of the male lobe) to

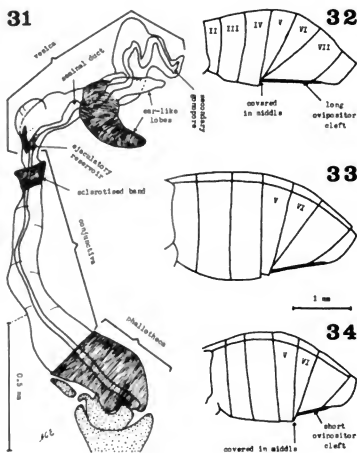


Fig. 31–34 Illustrating structural terms in *Rhypodes*. 31, aedeagus of *R. sericatus* ♂ (Kaikouras); 32–34 ♀ abdomen, side view; 32, *R. rupestris* n. sp. paratype; 33, *R. clavicornis* (Rimutakas); 34, *R. stewartensis* (Manapouri).

hold the male gonopore in the correct place (Fig. 126). The sclerotised lobe comes across from basally to hold the gonopore in place (on the opposite side to the terminal lobe) and may rest on the flange of the spermatheca to do this. The membranous ear-like lobe also helps in holding, either on the same side as the terminal lobe, or underneath between it and the sclerotised lobe. This may be why in *Rhypodes* the secondary gonopore is always between the two ear-like lobes and the terminal lobe. The membranous perimeter of the female genital chamber has small sclerotised spines and sclerotised ridges which no doubt facilitate this holding. Sometimes the secondary gonopore reaches into, or almost to the top of, the flange. The spermathecal duct above the flange was not uncoiled during copulation but was just resting on the flange.

Taxonomic characters

Characters most useful in distinguishing species are as follows:

1. Hairiness: presence or absence of semi-erect hairs on one or more parts of the body, and presence of very long outstanding hairs.
2. Spacing of pronotal punctures.
3. Colour of antennal segments and presence of spotted antennae.
4. Thickness and length of head in side view and whether the vertex is elevated above the eyes.
5. Length of rostrum.
6. Shape of pronotum including triangular and conical projections.
7. Colour of wings including the presence of a pale subapical corial spot (Fig. 37).
8. Length of ovipositor cleft and whether, in the female abdomen, sterna V, or V and VI are covered or uncovered in middle (Fig. 2, 32–34).
9. Shape and length of first antennal segment, and sometimes relative lengths of other segments.
10. Shape of parameres.
11. Shape and aspect of spermathecal bulb.
12. Shape of apex of scutellum.
13. Whether or not body is flattened.
14. Whether or not connexivum is broadly exposed.
15. Presence of slender femora.
16. Presence of distinctive head markings.
17. Prominent brachyptery leaving most of abdomen exposed.
18. Bucculae projecting forward beyond tip of tylus.

TAXONOMY

Systematic position of *Rhypodes*

The genus *Rhypodes* is placed in the tribe Nysiini Uhler (Ashlock 1967) of the lygaeid subfamily Osrillinae. The characters placing it in the subfamily include the last abdominal tergum in males greatly exceeding the connexivum posteriorly (Fig. 25) and overlapping claval apices (Ashlock & Slater 1976), the dorsal position of all abdominal spiracles, the straight ventral abdominal sterna sutures which all reach the lateral margin, the asymmetrical vesica with a large pigmented lobe near base and lacking a helicoid process (Ashlock 1967), and the two dorsal abdominal scent gland openings between segments IV and V and between V and VI.

The particular characters placing *Rhypodes* in the tribe Nysiini are: costal margin straight and parallel for a short distance not exceeding level of apex of scutellum, then expanded, in combination with a dorsal lobe on the conjunctiva of the aedeagus (Ashlock 1967).

Speciation and adaptive radiation within *Rhypodes* we produced some extraordinary forms (see "Limits the genus *Rhypodes*" following the genus description below) which now makes its placement the tribe Nysiini seem uneasy. Ashlock (1967) ated quite openly that there is no character found ily in this tribe. *Rhypodes* has punctate bucculae, a aracteristic of some Metargini, and often the nnexivum slightly or broadly exposed, a characteristic 'most Orsillini. *Rhypodes* also has punctures following +M and on the clavus, which occurs in both Nysiini and larargini. However, it is well known that similar aracters can evolve independently in different groups. he present author does not know the other orsilline nera sufficiently to make any definitive statement on bal classification, except that the characters herein scribed in these new species of *Rhypodes* will either low a new definition of the Nysiini to be formulated, r the placement of this genus in another tribe.

Ashlock (1967) greatly improved the tribal lassification of the Orsillinae, laying down a sound undation. He openly stated that it has weaknesses, nd reported exactly what he found, that some of the haracters of each tribe are present in one or more of e other tribes. There appear to be too many excep-ons. Perhaps too much weight is put on the punctate ucculae character, for all genera possessing it were laced in the Metargini, yet not all Metargini have . The shape of the costal margin of the forewing ay sometimes be a confusing character to use.

Although Ashlock stated that "there are no tructures in the orsilline spermatheca that haracterise the subfamily or its tribes" his figures aggest otherwise. Had more weight been given to his character some of the above problems may have een sorted out. It is suggested that in the future me other worker may like to redefine the tribes long the following lines which is based only on permathecae as figured in Ashlock (1967).

Nysiini: could be restricted to those genera without flange on the spermatheca and with a small bulb— *Nysius*, *Nesomartius*, *Oreonyx*, *Glyptonyx*, *Coleonyx*, *Darwinysius*, *Xyonyx*, *Balionysius*, nd *Robinsonocoris*. Note: *Robinsonocoris* (not igned) would probably also be placed here. Twice n his description of *Balionysius* and *Coleonyx*, Ashlock (1967) stated that they are similar to *Nysius*. Thus, such a revision might result in six genera aving to be transferred from the Metargini and in *Rhypodes* and *Nithecus* being excluded.

Orsillini: could comprise those genera with a permatheca similar to that in *Orsillus* having a single

lip to the flange (but retaining *Ortholomus*)—*Orsillus*, *Aborsillus*, *Belonochilus*, *Eurynysius*, *Austronysius*, *Hyalonysius*, *Ortholomus*, and *Oceanides*. Note: such a revision might result in transferring *Oceanides* (from Metargini) and in excluding *Camptocoris*.

Metargini: could be restricted to those genera with a lip at top and bottom of the flange (as in *Nesocryptias*) – *Metarga*, *Nesocryptias*, *Nesoclimacias*, *Neseis*, *Rhypodes*, *Nithecus*, and *Camptocoris*. Note: such a revision might result in *Rhypodes* and *Nithecus* having to be transferred from the Nysiini, *Camptocoris* from the Orsillini, and in the exclusion of seven genera, six of them perhaps going to the Nysiini.

Lepionysiini: spermatheca with a single asymmetrical flange on only one half of the duct – *Lepionysius*.

Until someone with a good working knowledge of the world genera is able to undertake a review, *Rhypodes* is left in its present systematic position, the Nysiini. As this is a generic revision the tribal classification, which is really outside the scope of the present study, will not affect it.

Rhypodes Stål

Rhypodes Stål 1868: 76 (Original description as subgenus of *Nysius*).

Hudsona Evans 1929a: 353 (New synonymy).

Myersia Evans 1929a: 353 (Synonym; syn. by Evans 1929b).

Rhypodes: Opinion 319 1955: (On official list generic names; fixes *Nysius zealandicus* as type sp.).

Rhypodes: Slater 1964: 343–344 (Catalogue).

Rhypodes: Ashlock 1967: 56 (Redescription, keyed, Figs. genitalia, in Nysiini).

Rhypodes: Eyles & Ashlock 1969: 715 (Distinguished from N.Z. *Nysius*).

Surface usually shiny. Colour dull brown, pale or variegated, with usually dark antennae and spotted or dark femora. Inner margin of eyes with a narrow pale orange or cream band; calli black.

Body form elongate oval and robust, to slender and parallel-sided; with appressed pubescence, and long hairs (at least on pronotum). Medium sized insects 4–8 mm long.

Head wider than long, may appear triangular, with antennal tubercles not or only just visible from above, or pentagonal with antennal tubercles clearly visible from above. Antecular length 1.1–2.15 × length of eye. Juga not reaching tip of tylus; either not prominent, lying close against sides of tylus

(Fig. 47), or prominent with a gap between tylus and each jugum, the points sometimes curving and jutting outwards (Fig. 174, 175). Vertex usually low, below or level with top of eye; in some species distinctly convex above eyes; rarely elevated in a prominent mound. Antennae with scattered erect hairs as well as shorter hairs; typical ratio of antennal segments 1.0 : 2.6 : 2.1 : 2.4; 1st segment with from 0–1/2 of its length projecting beyond tip of tylus. Dorsal surface with irregular wrinkles under pubescence; ventral surface punctate under pubescence. Bucculae finely or coarsely punctate; as long as or longer than width of rostrum; convex or flat to about level of antennal tubercle, where they taper, continuing as short, tapering carinae meeting and ending in a V or rounded V just before base of head. Rostrum reaching to form mid coxae to well beyond hind coxae.

Pronotum with lateral edges dorso-ventrally rounded; sides straight or sinuate; anterior margin concave; posterior margin convex before scutellum, with sinuation at each basal angle of scutellum. In some species posterior margin with two large, triangular, plate-like projections overlapping bases of clavi (Fig. 82); rarely with two pointed, conical projections on sides of pronotum at anterior (Fig. 40). Pronotum punctate; usually slightly convex, sometimes elevated posteriorly. Scutellum punctate; with tri-radiate elevation; apex acute or rounded, often turned up.

Hemelytra with costal margin more or less straight to about level of apex of scutellum, then slightly expanded and arcuate; connexivum of abdomen partly (usual) or broadly exposed, or unexposed. Point of branching of vein R+M between level of middle of claval commissure and apex of clavus (except in brachypters); the branches relatively long, with M closer to Cu than to R on apical margin. Clavus and disc of corium often lightly punctate; usually with row of faint punctures lateral to R+M at least basally; usually with full or part faint row on clavus following claval suture.

Legs short, hind femora rarely surpassing level of apices of coria; tibiae slightly longer than femora; hind tarsus with combined length of 2nd and 3rd tarsomeres (excluding claw) about equal to length of 1st tarsomere. Femora and tibiae often with erect or semi-erect hairs as well as shorter hairs or pubescence, especially on fore tibia where erect hairs are sometimes as long as, or longer than, width of tibia at middle.

Abdomen with spiracle VII in lateral third, sometimes on lateral margin, of connexivum; membrane between terga and inner laterotergites with tiny, sclerotised, tooth-like spines (Fig. 22).

Paramere blade varies from short and curved throughout (Fig. 56, 95) to long, straight for part of length and not tapering (Fig. 51, 106).

Aedeagus with 0–2 conjunctival lobes (Fig. 31, 114, 63). Vesica (Fig. 130, 172) with two large ear-like lobes (basal one sclerotised), another large, and one or two small, membranous lobes. Sometimes with small membranous lobe before ear-like lobes (Fig. 31, 54, 110). Seminal duct not free; secondary gonopore flared. Ejaculatory reservoir with broad triangular (Fig. 28), or A-shaped (Fig. 29), wings; body not apparent, fused with wings.

Spermatheca consisting of bulb, short duct and a large, cup-like flange; bulb may be elongate and lying over (as in type species, Fig. 27), round or lemon-shaped (as in *sericatus*, Fig. 163), or intermediate with a longer and disorganised duct (Fig. 161). Ring sclerites present on roof of genital capsule may be larger or smaller than spermathecal bulb (Fig. 26).

Type species. *Nysius zealandicus* Dallas 1852 = *Lygaeus clavicornis* Fabricius 1794.

Distinguished from *Nysius* Dallas 1852 by the presence of a flange on the spermatheca, and often by the broadly or narrowly exposed connexivum (unexposed in *Nysius*). *Rhyodes* is readily distinguished from New Zealand species of *Nysius* by the distinctly tapering bucculae behind level of antennal tubercle (not or scarcely tapering in New Zealand *Nysius* and ending abruptly near base of head), and by the larger size (except some specimens of *R. celmsiae* n. sp. and *R. anceps*).

N. zealandicus is the official name of the type species because Stål described *Rhyodes* using the Dallas specimens. However, the official name of the species is *clavicornis* as *zealandicus* is a synonym.

The characters of *Hudsona* fall within the range of variation found in *Rhyodes* (see immediately below).

LIMITS OF THE GENUS RHYPODES

Until the present study, insufficient species were known for previous workers to adequately describe the genus *Rhyodes* or to define its limits. The species *clavicornis* was soon transferred to *Nysius*, *anceps* was described in *Nysius*, and Ashlock (1967) stated that except for *clavicornis*, *Rhyodes* species are very difficult to separate from *Nysius*.

Rhyodes was separated from typical *Nysius* on account of the large, triangular, plate-like projections on the posterior lobe of the pronotum overlapping the bases of the clavi in the genotype. This is not a

eric character, but proves to be a good specific character, yet only three species possess it, so it is an unusual or rather remarkable character. Several times, perhaps bizarre characters occur within the genus, either in a single species or shared by two or three species, making *Rhyphodes* the most remarkable genus in the Orsillinae.

Furthermore, there are marked differences between the species, more so than occurs between species in other genera in this subfamily. The four species of *Rhyphodes* described by Usinger (1942b) differ so considerably from the genotype that, according to standards elsewhere in the world each could perhaps be made the type of a new genus." However, he wisely chose to lump them "into a single, possibly unnatural genus, until further material is at hand and more extensive fieldwork has been done." Among the 28 species there appeared to be several groupings of species within the genus, but when this was studied carefully there was no way of dividing the genus into separate genera because of species with some characters bridging the gaps.

Most of the species have a similar general appearance—a broad pronotum, with sides straightish, greatly tapering anteriorly and a body that is oval-shaped (Fig. 166) (thinking of a sports oval rather than egg-shaped or pear-shaped). The parameres have the blade short, curved throughout and tapering (Fig. 95), and the spermatheca with a long elongate and lying over (Fig. 27).

Two species *R. rupestris* n. sp. (Fig. 142) and *R. eminens* n. sp. (Fig. 102), that at first seemed as though they could be taken out as a separate genus, have a pronotum with sides sinuate, flaring to well eloped and elevated postero-lateral corners, which makes the body an egg-shaped appearance. The parameres (Fig. 106, 154) have the blade long and straight for part of its length, and not tapering. The spermatheca (Fig. 108, 156) has the bulb rounded lemon-shaped and standing upright. The mesence is very short, long erect hairs are absent (except on anterior pronotal lobe), the insect surface dull, and the body flattened. One of them has a prominent bump on the head.

However, two species, *R. sericatus* and *R. argenteus* n. sp., which have the external appearance of the first (or *clavicornis*) group, have the parameral spermathecal characters of the second (or *rupestris*) group (Fig. 30, 49, 51, 163). So these are specific, not generic characters. *R. argenteus* also has long pubescence. Further, one species, *R. brevipilis* n. sp., which on external characters would be placed in the *rupestris* group, has the short, curved, tapering

paramere of the first group (Fig. 69). The pronotum is not so elevated posteriorly. This species resembles *R. bucculentus* n. sp. which, in addition, has the bizarre character of the bucculae projecting forwards beyond tylus tip (Fig. 72). Both species have narrow femora.

R. rupestris and *R. eminens* do not form a separate genus because *R. sericatus* and *R. argenteus* are the link in one direction, and *R. brevipilis* the link in another direction, keeping them within the bounds of *Rhyphodes*. It should also be noted that *R. depilis* n. sp. has a flat pronotum with sinuate sides, and that *R. longiceps* n. sp. and some other species have a pronotum with sinuate sides.

There is perhaps an intermediate group of two narrow, slender species (Fig. 103, 143) with a spermathecal bulb intermediate between elongate and rounded, and a long, disorganised duct (Fig. 116, 161). The parameres have a blade of medium length, curved throughout and tapering (Fig. 113, 158).

R. clavicornis and *R. cognatus* n. sp. are unusual in the genus in exhibiting considerable sexual dimorphism. The females are oval-shaped, but the males are narrow and parallel-sided, almost like the slender intermediate species *R. gracilis* and *R. russatus*. The distinction is in the amount by which the pronotum at posterior is wider than the head, as shown in Table 1. Thus, *clavicornis* and *cognatus* are regarded as being oval-shaped (they are not slender), their narrow males being one link keeping the intermediate or slender group within the genus *Rhyphodes*.

A long ovipositor cleft with sterna V and VI in females both covered in the middle is a specific and not a generic character as it occurs not only in *rupestris* and *eminens*, but also in *sericatus*, *argenteus*, the slender group, and in *chinai* of the *clavicornis* or oval-shaped group.

Hairiness, or variations in distribution of erect or semi-erect hairs, is only a specific character within

Table 1 Comparison of species having narrower males with the two slender species.

Species	Amount pronotum wider than head (in mm)	
	♂	♀
<i>gracilis</i>	0.27	0.45
<i>russatus</i>	0.31	0.47
<i>clavicornis</i>	0.56	0.76
<i>cognatus</i>	0.48	0.64

the genus. There are two interesting examples where a species known from the South Island (*stewartensis*, *myersi*) has in its place an almost identical species in the North Island (*brevifissas* n. sp., *longirostris* n. sp.) distinguished by a covering of longer hairs.

There is one other subgroup within *Rhyphodes*, but these species simply have some characters nearer to one another than to other species, and at no stage was there any thought of taking them out of the genus. *R. stewartensis*, *brevifissas*, *crinitus* n. sp., and *jugatus* n. sp. look alike on account of the wide pronotum with coarse punctures widely spaced, and the broad body compared with its short length.

Thus, any character or characters that might take one or another group off as a separate genus occurs elsewhere in the genus. All the species belong in the one genus, *Rhyphodes*.

Hudsona was separated from *Nysius* on account of the brachyptery and elongate (not laterally dilated) abdomen, and more or less parallel-sided pronotum (Evans 1929a). Although not mentioned by Evans, the conical, pointed, lateral projections at anterior of pronotum (Fig. 40) on the single species then known were used as one of the distinguishing characters of that genus (Usinger 1942b; Ashlock 1967). *R. brachypterus* n. sp. lacks these projections, proving that this bizarre character is specific, not generic. In the present work *Hudsona* is synonymised with *Rhyphodes*.

Brachyptery alone is not sufficient for its standing as a separate genus. Two new species, *R. celmisiae* and *R. jugatus*, have some sub-brachypterous specimens. Also *Nysius* in New Zealand contains macropterous and sub-brachypterous forms (Eyles 1960a; Eyles & Ashlock 1969). Other unusual characters like the pronotal projections are found in *Rhyphodes*. The convex vertex is found in *R. myersi* and *R. atricornis* n. sp. to name two examples, and the spermatheca (Fig. 46), paramere (Fig. 43), and aedeagus (Fig. 45) fall within the range of variation found in *Rhyphodes*. In general, *Hudsona* seems no different from any of the other considerable variation within *Rhyphodes* as explained above.

KEY TO THE SPECIES OF RHYPODES

- 1 With prominent bump on head (Fig. 102, 105) *eminens* n. sp.
- Without prominent bump on head 2
- 2 Brachypterous, wings greatly reduced, most of abdomen uncovered 3
- Macropterous, wings fully developed, covering abdomen 4

- 3 With pointed projections on sides of pronotum at anterior (Fig. 40); often mainly pale straw coloured, including antennae and femora *anceps* (White)
- Without pointed projections on sides of pronotum at anterior; usually black, including antennae and femora *brachypterus* n. sp.
- 4 With two large triangular, plate-like projections on posterior margin of pronotum overlapping bases of clavi (Fig. 82) 5
- Without two large triangular, plate-like projections on posterior margin of pronotum 7
- 5 Hemelytra brown, sometimes variegated, without pale subapical corial spot; rostrum reaching mid coxae (Fig. 85) *clavicornis* (Fabricius)
- Hemelytra mostly pale or buff, with pale subapical corial spot; rostrum reaching hind coxae 6
- 6 Third antennal segment bright yellow in apical third; in ♀ only sternum VI covered in middle (Fig. 169) *triangulus* n. sp.
- Third antennal segment with a narrow, pale, apical band; in ♀ sternum V and VI covered in middle (Fig. 83) *chinai* Usinger
- 7 Bucculae projecting forwards beyond tip of tylus (Fig. 72), this part visible from above *bucculentus* n. sp.
- Bucculae not projecting forwards beyond tip of tylus and not visible from above 8
- 8 With slender body in both sexes (Fig. 103, 143); pronotum at posterior only slightly wider than head (see Table 1); spermatheca with long, disorganised duct (Fig. 116) 9
- With body not slender, but oval- or egg-shaped; if body narrow in males only, e.g., *cognatus*, then pronotum at posterior considerably wider than head (0.45–0.50 mm in ♂, much more in ♀); spermatheca with short duct (Fig. 99, 108) 10
- 9 Red, with a narrow, longitudinal, pale stripe on lamellate costal margin only (Fig. 143) *russatus* n. sp.
- Greyish brown, with a wider longitudinal, pale stripe extending onto corium as far as vein R+M and apically, to the inward curving vein R (Fig. 103) *gracilis* n. sp.
- 10 With a pale subapical corial spot (Fig. 37) 11
- Without a pale subapical corial spot 13
- 11 Antennae spotted (segments I–III); 2nd antennal segment mostly pale; rostrum reaching mid coxae (Fig. 144) *sericatus* Usinger
- Antennae without spots; 2nd antennal segment dark throughout; rostrum reaching hind coxae 12

- Mottled, with pale spots on basal two-thirds of corium and apical half of clavus; lengths of 3rd and 4th antennal segments subequal; pubescence long (Fig. 37) *argenteus* n. sp.
- Not mottled, with corium and clavus mostly pale; 4th antennal segment distinctly longer than 3rd segment; pubescence not long (Fig. 83) *chinai* Usinger
- With erect or semi-erect hairs on hemelytra either well distributed (usual) or near base of clavus and corium only (*atricornis* only) 19
- Without erect or semi-erect hairs on hemelytra 14
- Rostrum reaching mid coxae; head in side view short, with dorsal surface declivous (Fig. 175, 166) *stewartensis* Usinger
- Rostrum reaching hind coxae or beyond; head in side view long, with dorsal surface not or only slightly declivous 15
- Clavus and corium brightly variegated throughout with pale spots on brown; dorsum of head deeply wrinkled; (5.85–7.20 mm long) (Fig. 168) *townsendi* n. sp.
- Clavus and corium not variegated, almost uniform in colour (some specimens of *rupestris* have small pale spots on part of corium); dorsum of head not or lightly wrinkled 16
- Punctuation on posterior pronotal lobe dense; smaller insects 4.55–6.35 mm long 17
- Punctuation on posterior pronotal lobe widely spaced; larger insects 6.5–8.3 mm long 18
- Fore femur slender (Fig. 68); rostrum reaching anterior of hind coxae; erect hairs present on posterior lobe of pronotum (Fig. 60) *brevipilis* n. sp.
- Fore femur not slender; rostrum reaching a little beyond hind coxae; without erect hairs on posterior lobe of pronotum (Fig. 142) *rupestris* n. sp.
- Semi-erect hairs on head and pronotum well distributed; 2nd and 3rd antennal segments with a bright pale band at apex (Fig. 140) *myersi* Usinger
- Semi-erect hairs on dorsum of head near eyes only, and on pronotum on extreme anterior margin only; 2nd and 3rd antennal segments with a narrow pale band at apex (Fig. 101) *depilis* n. sp.
- Semi-erect hairs on head near eyes only and on hemelytra near base of clavus and corium only; antennae black throughout (Fig. 38) *atricornis* n. sp.
- Semi-erect hairs well distributed on head and hemelytra; antennae not black throughout 20
- 20 All tibiae with many long outstanding hairs, longer than width of tibia at middle (Fig. 4, 6) 21
- At least hind tibiae without long outstanding hairs. (If appearing to be present on hind tibia, e.g., *longirostris*, then there are more short than long hairs, or they are only equal to, not longer than, width of tibia at middle.) 23
- 21 Second and 3rd antennal segments dark with a pale band at apex; embolium pale in at least basal half (Fig. 88) *crinitus* n. sp.
- Second and 3rd antennal segments mostly pale or orange; embolium not pale, or pale in basal quarter only 22
- 22 Second antennal segment orange, with a dark band at apex and base; punctuation on posterior pronotal lobe dense (Fig. 104) *hirsutus* n. sp.
- Second antennal segment pale, usually with a narrow dark band at base; punctuation on posterior pronotal lobe widely spaced (Fig. 59) *brevifissus* n. sp.
- 23 Punctuation on posterior pronotal lobe dense; vertex rather flat, not elevated above top of eyes 24
- Punctuation on posterior pronotal lobe widely spaced; vertex distinctly convex above level of top of eyes 27
- 24 Rostrum reaching mid coxae (Fig. 87) *cognatus* n. sp.
- Rostrum reaching hind coxae 25
- 25 Head pale orange, with distinctive black markings in posterior half (Fig. 128); punctures on pronotum shallow, fine; 1st antennal segment mostly pale orange (Fig. 121) *koebelei* n. sp.
- Head black; punctures on pronotum deeper, coarse; 1st antennal segment black or mostly black 26
- 26 Head in side view with portion between front of antennal tubercle and tip of tylus gradually tapering, so that head appears longer and narrower (Fig. 132); body narrower and greyish (Fig. 123) *longiceps* n. sp.
- Head in side view with portion between front of antennal tubercle and tip of tylus blunt or tilted down, so that head appears shorter and stouter (Fig. 170); body wider, more oval, brown (Fig. 164) *spadix* n. sp.
- 27 Small insects 4.0–5.7 mm × 1.5–2.2 mm; bucculae black or mostly black; wings with black rectangles leading to a black X on membrane (Fig. 62) *celmisiae* n. sp.

- Larger insects 5.5–7.3 mm × 2.1–2.8 mm; bucculae pale; wings pale, without the above distinctive black markings 28
- 28 Pronotum with 4 longitudinal black stripes; 1st rostral segment reaching base of head; tibiae with outstanding hairs, long on fore and mid tibiae (Fig. 124) *longirostris* n. sp.
- Pronotum without longitudinal black stripes; 1st rostral segment not reaching base of head; tibiae with short hairs at a more acute angle (Fig. 120) *jugatus* n. sp.

SPECIES DESCRIPTIONS

In the descriptions all measurements are in mm, those of females given in brackets (except where no male specimens were available). The specimens were tilted so that the various parts were brought into the horizontal plane, for example when measuring length of head (and parts of the head such as distance between anterior of eye and base of antenna), pronotum, and antennal segments. Five specimens of each sex, or the number available when less than five, were measured. However, under "size" the range over all specimens is given.

When checking specimens for hairiness or lack of hairs it is advisable to examine several specimens. If specimens have been cleaned for any reason, or if there were too many in the tube when collected, or they were left too long before being killed, long erect hairs may have been rubbed off. Usually, however, some are left, or at least some stumps, as evidence of the presence of erect or semi-erect hairs. For this reason care should be taken when collecting these bugs, to ensure that specimens are in very good condition.

In the descriptions the following characters are mentioned only when present and not when absent, because they occur in comparatively few species: 1 flattened body; 2 special kind of pubescence; 3 brachypterous and sub-brachypterous forms; 4 triangular, plate-like projections on posterior margin of pronotum overlapping bases of clavi; 5 lateral, conical projections at anterior of pronotum; 6 antenniferous tubercles which are black throughout (In most species they are pale or orange at least at the tip on the underside.); 7 placement of spiracle VII on or very near lateral margin (In most species it is in a more central position – in lateral third or quarter.); 8 vein 1A joining PCu on the membrane.

All species have erect hairs on the anterior pronotal lobe, so this is not mentioned in the

descriptions. Most species have erect or semi-erect hairs on the dorsum of the head, posterior pronotal lobe, and scutellum, and a tuft of long hairs laterally at base of costal margin. Therefore, to avoid much repetition, these characters are mentioned in the descriptions only in the four or five species in which they are absent (and in the three species in which the outstanding hairs are very long).

Abbreviations for repositories

AMNZ—Auckland Institute and Museum, Auckland, New Zealand.
BMNH—British Museum of Natural History.
CASC—California Academy of Sciences.
CMNZ—Canterbury Museum, Christchurch, New Zealand.
FRNZ—Forest Research Institute, Rotorua, New Zealand.
GGES—G. G. E. Scudder collection, Vancouver.
NMNZ—National Museum, Wellington, New Zealand.
NZAC—New Zealand Arthropod Collection, DSIR Plant Protection (formerly Entomology Division, DSIR), Auckland.
TFPM—Taranaki Forest Park Museum, Otaki, New Zealand.
USNM—United States National Museum.

The two letter area codes, e.g., AK for the Auckland area, NN for the Nelson area, are those proposed by Crosby et al. (1976).

Rhyodes anceps (White) new comb. (Fig. 35, 36, 40–46)

Nysius anceps White 1878: 32–33 (Original description).

Hudsona anceps: Evans 1929a: 353 (New genus).

Hudsona anceps: Usinger 1942b: 42–43 (Keyed, note).

Hudsona anceps: Slater 1964: 239–240 (Catalogue).

Hudsona anceps: Ashlock 1967: 32 (Redescription, keyed, Figs including genitalia, in Orsinillini).

Hudsona anceps: Wise 1977: 122 (List).

Hudsona anceps: Ueshima & Ashlock 1980: 726, 735, 782, 793 (Chromosomes including Figs).

Characterised by the pointed, lateral pronotal projections, brachyptery, moderately swollen femora, and often by the pale straw colour including antennae and femora.

Colour. Pale straw coloured and brown; shiny. Head dark brown, with pale yellow or orange markings (Fig. 40) as follows: band following inner



Fig. 35 *Rhyodes anceps* (White) ♂ (Mt Altmarlock).

margin of eyes, with a branch to ocelli; mid-longitudinal stripe in basal half; 2 spots in front running forward to jugs and sometimes part of tylus. 1st antennal segment mostly pale, at least in basal half; 2nd segment pale, with dark apex; 3rd segment light brown, with paler apex; 4th segment dark. Pronotum and scutellum with mid-longitudinal pale stripe; pronotum with 4 longitudinal brown stripes, cutellum with 2; basal angles of scutellum brown. Dorsal surface of abdomen with a broad, mid-longitudinal brown stripe and usually 2 lateral brown stripes. Ventral surface with a pale stripe from antenniferous tubercles through thorax and abdomen. Femora yellow, with brown spots; tibiae pale, sometimes darker at apex.

Structure. Size: ♂ – length 4.4–5.2, width 1.35–1.7; ♀ – length 4.5–5.85, width 1.72–2.2. Form oval narrower in ♂; brachypterous, wings greatly reduced, most of abdomen exposed (Fig. 35). Hemelytra with semi-erect hairs well distributed.

Head width to length 1.21 : 0.92 (1.30 : 1.02). Eye length 2.4× distance between anterior of eye

and base of antenna, 0.41 : 0.17 (2×, 0.4 : 0.2). Width of vertex 2.5× eye width, 0.67 : 0.27 (3.2×, 0.80 : 0.25); vertex convex above level of top of eyes; jugs not prominent. Antennal segments 0.32 : 0.70 : 0.57 : 0.73 (0.32 : 0.69 : 0.55 : 0.72); 1st segment with about one-sixth (♀ about one-eleventh) of its length projecting beyond tip of tylus. Head in side view (Fig. 41) short and thick. Rostrum reaching mid coxae; 1st segment not reaching base of head.

Pronotum width to length 1.28 : 0.81 (1.42 : 0.89); in both sexes only slightly wider at base than head; sides straightish, not suddenly tapering anteriorly; with 2 pointed, conical projections laterally at anterior (Fig. 40); punctation on posterior lobe shallow and widely spaced. Scutellum width to length 0.77 : 0.55 (0.93 : 0.60); apex rounded, level. Clavus fused with corium; level of branching of R+M at apex of scutellum. Femora moderately swollen.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 43) with blade short, curved throughout, not tapering. Aedeagus (Fig. 45) without conjunctival lobe; secondary gonopore not flared; ejaculatory reservoir (Fig. 44) with large, broad wings.

Spermatheca (Fig. 46) with bulb rounded; duct long; lip of flange appearing to project more on one side.

Material examined. 296 specimens (CMNZ, FRNZ, NMNZ, NZAC).

Diagnosis. Distinguished from *R. brachypterus* n. sp. by the pointed, lateral pronotal projections behind eyes, and often by the pale straw colour including antennae and femora.

Distribution. A lowland and mountain species, occurring from sea level, along roadsides, to 1950 m, throughout the South Island including Stephen's Island, and around Wellington city (Fig. 36). No specimens north of Wellington have been seen, a situation also noted by Myers (1926). Although no specimens were seen from Buller, Dunedin, and Westland, Myers recorded it from Greymouth. Barratt & Patrick (1987) record this species from the East Otago Plateau. So far *anceps* has not been collected from Stewart Island.

Biology. Taken on *Raoulia tenuicaulis* on a scree in Head Basin, Takahe Valley, FD. This is a definite host association as there were no other plants around. As it was taken on *Raoulia* mats on six other occasions in six different localities, and as other species of



Fig. 36 Distribution of *Rhypodes anceps* (White).

Rhypodes breed on this plant, *R. anceps* no doubt lives on it too. Taken on *Celmisia spectabilis* subsp. *spectabilis*, Mt Percival, KA; *C. prorepens*, Old Man Range, CO, at 4500 ft (1372 m); and *Celmisia* sp. Sentinel Peak, Young Range at 1370–1524 m (near Lake Wanaka). Other species are known to breed on *Celmisia* species. As adults and nymphs were taken on roadside grass and weeds, notably sorrel, between Lakes Tekapo and Pukaki, they were breeding there. Kelsey (1957) recorded this species feeding on the leaves of tussock. In the present study it was associated with tussock in five localities: Stephen's Island, SD, and SW of Ward's Pass, MB, 5000 ft (1524 m), sweeping tussock; Coronet Peak and Queensbury, OL, in tussock debris; Black Birch Range, MB, 1690 m, on *Chionochloa macra*. In three additional localities such as Hokonui Hills, SL, "sweeping" probably refers to sweeping tussock. Six adults were taken under *Epilobium porphyrium* at 5200 ft (1584 m), Mt Hutt. Low numbers of adults have also been taken on *Haastia pulvinaris* flowers, *Muehlenbeckia*, snow grass (*Danthonia flavescens*), *Dracophyllum muscoides*, tall bracken, rushes, and under *Aciphylla squarrosa*. See also Tables 3 and 4.

Remarks. No macropters are known. Typical for sides of pronotum (excluding lateral projections), but spermatheca as in *R. rupestris* n. sp. and paramere shape intermediate between *rupestris* and the type. There is variation within the species. Intensity of colour of the first three antennal segments varies. Size varies, some high altitude specimens being

small and much darker, sometimes mostly black. The smallest measure: ♂ 3.2 × 1.2 mm, ♀ 4.21 × 1.58 mm. The pronotal projections vary. Although many specimens have long, conical projections (Fig. 40), in some they are shorter and blunt (Fig. 42). However, the projections are always prominent and almost invariably present. Their absence is extremely rare — only 2 specimens out of 296, both females of the usual pale colour, had no pronotal projections. One from Coronet Peak in a series of 40 and one from Niger Peak, OL, 6000 ft (1830 m) in a series of three. Two ♀ Coronet Peak, 1 ♂ Old Man Range, CO and 1 ♂ Mt Owen, NN, had a projection on one side only. One ♂ Coronet Peak and 1 ♂ Takah Valley had small projections.

***Rhypodes argenteus* n. sp.**
(Fig. 37, 47–53)



Fig. 37 *Rhypodes argenteus* n. sp. holotype ♂.

characterised by the pale subapical corial spot, titled wings, long, dense, silvery grey pubescence, l shape of parameres.

Colour. Mottled white on black, with silvery grey pubescence; shiny. Head black, with a broad white line on edges of vertex; 1st and 4th antennal segments black; 2nd segment either with a broad, low band before apex, or black throughout; 3rd segment mostly pale, with a dark band at base sometimes brown extending nearly to apex). Pronotum with 3 black spots behind calli and 4 black spots across posterior. Scutellum sometimes with 2 black spots near base. Hemelytra brightly mottled with small pale spots on apical half of clavus and apical two-thirds of corium; corium with large pale apical spot (Fig. 37). Femora yellow with black spots (merging near apex); fore femora in ♂ mainly black; all femora with a conspicuous yellow spot at apex; tibiae pale, with small dark spots and a black band at apex and near base.

Structure. Size: ♂ – length 5.3–5.8, width 1.8–2.0; ♀ – length 5.8, width 2.0–2.1. Form oval; body tapered; connexivum often not showing, but in the ♂ narrow, outer part exposed. Covered with long, dense pubescence; hemelytra with semi-erect hairs near base of clavus and corium only.

Head width to length 1.27 : 1.06 (1.34 : 1.18). Eye length 1.35× distance between anterior of eye to base of antenna, 0.35 : 0.26 (1.17×, 0.35 : 0.30). Length of vertex 3× eye width, 0.75 : 0.25 (3.4×, 0.85 : 0.25); vertex not elevated above eyes; juga not prominent (Fig. 47). Antennal segments 0.46 : 0.87 : 0.54 : 0.67 (0.45 : 0.88 : 0.68 : 0.70); 1st segment about half (♀ one-fourth) of its length projecting over tip of tylus. Head in side view (Fig. 48) tapering long and narrow. Rostrum reaching hind tibiae; 1st segment reaching beyond base of hind tibiae.

Pronotum width to length 1.81 : 1.12 (1.95 : 1.0); sides straightish, not suddenly tapering anteriorly; punctuation on posterior lobe shallow, widely spaced. Scutellum width to length 1.02 : 0.82 : 0.5 : 0.88; apex rounded, upturned.

In ♀, abdominal sterna V and VI covered in black; ovipositor cleft more than half as long as omen.

Genitalia. Paramere (Fig. 51) with blade long, broad, light for part of its length, not tapering. Aedeagus in Fig. 53; ejaculatory reservoir as in Fig. 52.

Spermatheca (Fig. 49) with bulb rounded or onion-shaped. Ring sclerites (Fig. 50) with basal der slightly wider, wavy, darker.

Type data. Holotype ♂ (5.8 × 1.95 mm), MK, Benmore Hydro road, 1500 ft (475 m) on *Raoulia* mats, 18 Jan 1966, J. I. Townsend (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (7 ♂ 1 ♀; BMNH, NZAC, USNM): 3 ♂ 1 ♀ same data as holotype; 4 ♂ same data except 2000–3000 ft, A. C. Eyles.

Other material examined. 1 ♂ same data as holotype, but left out of type series because the adult has not emerged properly. It has the long, broad paramere of this species (NZAC).

Diagnosis. *R. argenteus* n. sp. is similar to *R. sericatus* Usinger, in shape of spermatheca and parameres and presence of dense silvery grey pubescence (silky white in *sericatus*), but is distinguished from it by the strikingly mottled (pale spots on black) basal two-thirds of corium and apical half of clavus, the mostly black second antennal segment, and longer rostrum.

Distribution. So far known only from the Mackenzie area.

Biology. Taken on, and probably lives on, *Raoulia*.

Remarks. Typical for sides of pronotum, but genitalia are as in *R. rupestris* n. sp. The only species with long pubescence.

Rhyodes atricornis n. sp.

(Fig. 18, 23, 38, 54–56)

Characterised by the black antennae, long 4th antennal segment and convex vertex.

Colour. Mostly brown; shiny. Head black; antennae black throughout (Fig. 38); bucculae cream to light brown, with brown line following base; antenniferous tubercles black throughout. Pronotum with punctures dark. Scutellum with a mid-longitudinal pale stripe in apical half. Hemelytra uniformly brown or with small, pale spots. Femora dark brown; tibiae dark at apex and base.

Structure. Size: ♂ – length 5.7–6.2, width 2.15–2.40; ♀ – length 5.9–6.8, width 2.35–2.70. Form oval; connexivum usually unexposed in both sexes (extreme outer edge exposed in some ♀). Spiracle VII on lateral edge of connexivum (Fig. 23). Semi-erect hairs on dorsum of head near eyes only, and on hemelytra near base of clavus and corium only.

Head width to length 1.3 : 1.09 (1.39 : 1.19). Eye length 1.6× distance between anterior of eye and base of antenna, 0.39 : 0.25 (1.5×, 0.40 : 0.27). Sides of head between anterior of eye and base of antenna



Fig. 38 *Rhypodes atricornis* n. sp. paratype ♀ (Takahe V).

diverging. Width of vertex $2.8 \times$ eye width, $0.75 : 0.27$ ($2.75 \times, 0.79 : 0.29$); vertex convex above level of top of eyes; jugs prominent. Antennal segments $0.44 : 0.86 : 0.73 : 0.90$ ($0.43 : 0.89 : 0.73 : 0.96$); 1st segment with one-fourth of its length projecting beyond tip of tylus. Head in side view appearing shortish and thick. Rostrum reaching mid coxae; 1st segment not reaching base of head.

Pronotum width to length $1.95 : 1.24$ ($2.19 : 1.30$); sides straightish, not suddenly tapering anteriorly; punctation on posterior lobe coarse, widely spaced. Scutellum width to length $1.09 : 0.85$ ($1.34 : 0.92$); apex acute, level. Membrane with 1A joining PCu (Fig. 18) in ♀ (except one), but not all ♂.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft less than half as long as abdomen.

Genitalia. Paramere (Fig. 56) with blade short, curved throughout, tapering. Aedeagus as in Fig. 54; vesica with a small membranous lobe before the sclerotised lobe; ejaculatory reservoir (Fig. 55) with wings more or less triangular, curled at edges.

Spermatheca (Fig. 54) with bulb elongate, narrow, lying over; flange with upper lip rolled.

Type data. Holotype ♂ (6.15×2.40 mm), FD, Head Basin, Takahe Valley, on *Raoulia tenuicaulis* on scree, 11 Dec 1972, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC).

Paratypes (5 ♂ 5 ♀; BMNH, NZAC, USNM): 3 ♂ 3 ♀ same data as holotype (3 taken under stone on scree); 2 ♂ 2 ♀ Wilmot Pass summit, 640 m, under *Epilobium pedunculare*, Jan 1970, A. C. Eyles, Manapouri Expedition.

Other material examined. 1 ♂ FD, above Homer Tunnel, 4300 ft (1310 m), general beating, 13 Jan 1967, A. K. Walker (NZAC).

Diagnosis. *R. atricornis* n. sp. is distinguished from *R. depilis* n. sp. and *R. myersi* Usinger by the fourth antennal segment which is longer than the second segment, and by the completely black antennae.

Distribution. Fiordland, at medium to high altitude.

Biology. Probably breeds on *Raoulia* and *Epilobium*.

Remarks. Genitalia and sides of pronotum typical.

Rhypodes brachypterus n. sp.
(Fig. 25, 39, 57, 58, 63)



Fig. 39 *Rhypodes brachypterus* n. sp. paratype ♀.

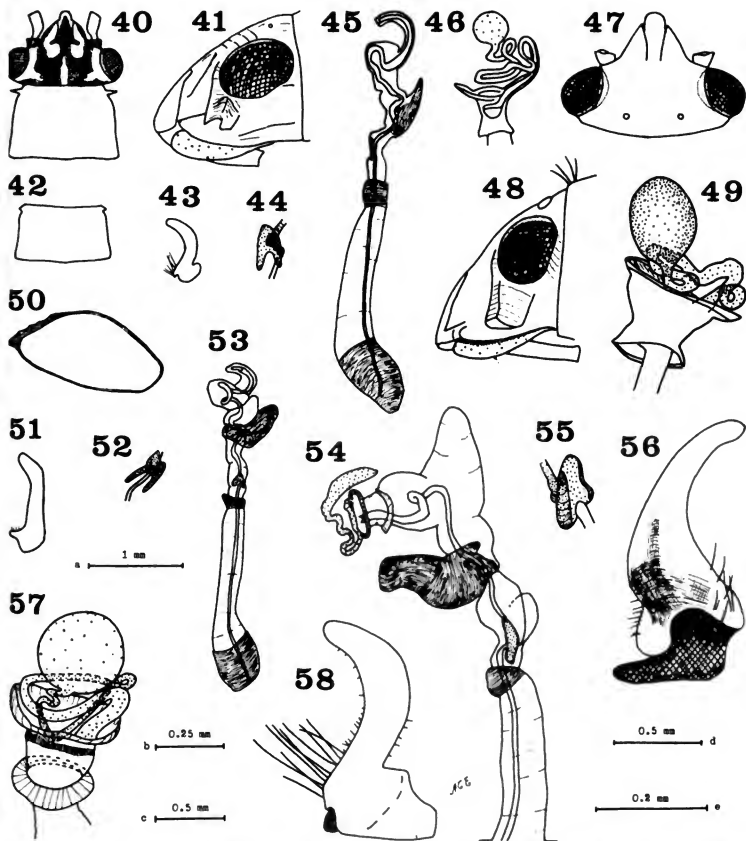


Fig. 40-58 40-46 *R. anceps*: 40, head, pronotum; 41, head, side view (both ♂ Timaru); 42, pronotum ♂ (Ben Nevis); 43, right paramere; 44, ejaculatory reservoir; 45, aedeagus (all ♂ Mt Snowflake); 46, spermatheca ♀ (Stephen's I.); 47-53 *R. argenteus* n. sp.: 47, head, dorsal view; 48, head, side view (both of paratype ♂); 49, spermatheca; 50, ring sclerite (both of paratype ♀); 51, right paramere; 52, ejaculatory reservoir; 53, aedeagus (all of paratype ♂); 54-56 *R. atricornis* n. sp.: 54, aedeagus and spermatheca of pair killed, dissected in cop; 55, ejaculatory reservoir ♂; 56, left paramere ♂ (all paratypes, Takahē valley); 57-58 *R. brachypterus* n. sp.: 57, spermatheca ♀; 58, left paramere, ventral view ♂ (both paratypes). Fig. 40, 42 to scale a; 46 to scale b; 47 to scale c; 41, 43, 45, 48, 51, 53 to scale d; 44, 52 to twice scale d; 49, 50, 55-58 to scale e; 54 to half scale e.

Characterised by the brachyptery, lack of pointed, lateral pronotal projections at anterior, flattened body, moderately swollen femora, and usually by the black colour including antennae and femora.

Colour. Black throughout including antennae and legs; shiny. With pale areas as follows: mid-longitudinal stripe on pronotum, back of head and apex of scutellum; sublateral stripe on pronotum; apices of femora; coxal covers; sometimes 2 spots on head between front of eyes. Tibiae brown.

Structure. Size: ♂ – length 4.95–5.15, width 1.75–1.80; ♀ – length 5.3–5.5, width 2.05–2.17. Form oval (narrower in ♂); body flattened; brachypterous, wings greatly reduced, leaving most of abdomen exposed (Fig. 39). Hemelytra with semi-erect hairs well distributed.

Head width to length 1.28 : 0.97 (1.35 : 0.99). Eye length 2.45× distance between anterior of eye and base of antenna, 0.44 : 0.18 (1.8×, 0.39 : 0.22). Width of vertex 2.15× eye width, 0.67 : 0.31 (2.55×, 0.77 : 3.00); vertex convex above level of top of eyes; juga not prominent. Antennal segments 0.31 : 0.65 : 0.52 : 0.74 (0.32 : 0.62 : 0.50 : 0.74); 1st segment with one-sixth (♀ none) of its length projecting beyond tip of tylus. Head in side view shortish and thick. Rostrum reaching mid coxae; 1st segment not reaching base of head.

Pronotum width to length 1.41 : 0.95 (1.58 : 1.02); in both sexes only slightly wider at base than head; sides straightish to slightly sinuate, not suddenly tapering anteriorly; punctation on posterior lobe coarse, widely spaced. Scutellum width to length 0.89 : 0.61 (1.00 : 0.71); apex acute, level. Clavus fused with corium; level of branching of R+M at apex of scutellum. Femora moderately swollen.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 58) with blade short, curved throughout, not tapering. Aedeagus (Fig. 63) with 2 small, membranous, subapical lobes on conjunctiva; vesica with 3 main lobes (one sclerotised) and a small lobe basally; ejaculatory reservoir large, triangular.

Spermatheca (Fig. 57) with bulb rounded; duct long.

Type data. Holotype ♂ (5.10×1.77 mm), NN, Mt Arthur, 1767 m (5800 ft), under *Helichrysum*, 23 Mar 1971, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (13 ♂ 14 ♀; BMNH, NZAC, USNM) all Mt Arthur: 5 ♂ 6 ♀ same data as holotype; 1 ♂ 1432 m, under *Aciphylla*, 22 Mar 1971, A.C.E.; 4 ♂ 4 ♀ 1680 m, 19 Nov 1969, J.I. Townsend;

1 ♂ 1710 m, on mat plants, 19 Nov 1969, J.I.T.; 1 ♀ 1500 m, on *Ranunculus* flowers, 16 Nov 1969, J.I.T.; 2 ♂ 2 ♀ 1650 m, 19 Nov 1969, B. M. May; 1 ♀ 4500 ft (1372 m), 2 Feb 1923, A. Philpott.

Diagnosis. *R. brachypterus* n. sp. is distinguished from *R. anceps* by the absence of pointed, lateral pronotal projections behind eyes, flattened body, and usually by the black colour including antennae and femora.

Distribution. A high altitude species so far collected only from Mt Arthur.

Biology. There is a definite association with *Helichrysum* on which other species of *Rhyodes* breed. It may also live on *Raoulia* and *Aciphylla*.

Remarks. No macropters are known. Typical for sides of pronotum, but spermatheca as in *R. rupestris* n. sp. and paramere shape intermediate between *rupestris* and the type. In contrast with *R. anceps*, which always has pronotal projections (their absence is so rare as to be of no significance), here we have a series of 29 specimens of *R. brachypterus* all without projections and all from Mt Arthur. They were collected over a 50 year time span, 1923–1971. Only three specimens have a slight hint of projections, but nothing like the prominent projections of *anceps*. Only two specimens are paler, the wings being buff, but not the abdomen. The pronotum is partly pale in one. The femora and antennae are dark, and the antennae of one specimen are dark. In the Philpott specimen the antennae are missing except for the first segment, which is black. These two specimens and one other have pale head markings. *R. brachypterus* does not appear to have adapted to such a wide range of food plants nor to have spread as widely as has *R. anceps*.

Rhyodes brevifissas n. sp. (Fig. 21, 59, 64–66)

Characterised by the long, outstanding hairs on all tibiae, widely spaced punctures on posterior pronotal lobe, and pale 2nd and 3rd antennal segments (Fig. 59).

Colour. Mostly pale, with some black; shiny. Head black; 1st antennal segment black, with pale base; 2nd and 3rd segments pale, usually with a narrow dark band at base; 4th segment black. Pronotum mostly pale buff, with brown punctation; calli surrounded by variable brown area. Scutellum black, with a mid-longitudinal pale stripe in apical half. Clavus and corium lightly variegated, with small.



fig. 59 *Rhyodes brevifissas* n. sp. paratype ♂ (Kawekas).

ale circles on brown. Membrane often smoky brown between veins, with small, pale spots, but sometimes clear. Femora spotted (brown spots on pale background); tibiae mostly pale except basally and apically.

Structure. Size: ♂ – length 4.85–5.60, width 1.94–2.00; ♀ – length 5.75–6.50, width 2.26–2.50. Form oval; connexivum at least partly exposed in both sexes. Spiracle VII in outer sixth of connexivum. Hemelytra with semi-erect hairs well distributed; all tibiae with long, outstanding hairs.

Head width to length 1.27 : 0.95 (1.33 : 0.99). Eye length 1.85× distance between anterior of eye and base of antenna, 0.35 : 0.19 (1.75×, 0.37 : 0.21). Width of vertex 2.6× eye width, 0.73 : 0.28 (2.8×, 1.78 : 0.28); vertex not elevated above eyes; jugal process prominent. Antennal segments 0.45 : 0.87 : 0.70 : 1.95 (0.45 : 0.83 : 0.67 : 0.90); 1st segment with half ♀ four-ninths of its length projecting beyond tip of stylus. Head in side view short and thick, dorsum somewhat declivous. Rostrum reaching mid coxae, 1st segment reaching base of head.

Pronotum width to length 1.88 : 1.19 (2.14 : 1.32); sides straightish, not suddenly tapering anteriorly; punctuation on posterior lobe coarse, widely spaced. Scutellum width to length 1.08 : 0.84 (1.26 : 0.98); apex acute, upturned.

In ♀, abdominal sternite V and VI uncovered in middle; ovipositor cleft less than half as long as abdomen.

Genitalia. Paramere (Fig. 65) with blade short, curved throughout, tapering; bearing ridges, end view of ridges like small teeth. Vesica of aedeagus (Fig. 64) with about 2 lobes in addition to sclerotised lobe; ejaculatory reservoir with small, reduced wings.

Spermatheca (Fig. 66) with bulb elongate and lying over; flange with upper lip flat.

Type data. Holotype ♂ (5.12×1.94 mm), HB, creek near Middle Range of Kaweka Range, 2850 ft (870 m), under *Epilobium komarovianum*, 27 Feb 1971, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (6 ♂ 6 ♀; BMNH, FRNZ, GGES, NMNZ, NZAC, USNM): 5 ♂ 1 ♀ same data as holotype; 1 ♀ BP, Tarawera, 11 Jul 1919, labelled “*Nysius clavicornis* (Fabr.)”, Det. J. G. Myers”; 1 ♀ BP, Pangitiki Land Development Plantation, on *Pinus radiata*, 16 Dec 1959, N.A.N., FRI 28; 1 ♂ RI, Ohakune, 1923, T. R. Hauio; 1 ♀ WN, Mt Hector, 4500 ft (1372 m), Tararua Forest Park, 15 Feb 1921, labelled “*Nysius clavicornis*”; 1 ♀ WN, Tauherenikau Valley, 24 Apr 1921, labelled “*Nysius clavicornis* (Fabr.)”, Ex W. Downs collection, donated 1958”; 1 ♀ Wilton’s Bush, Wellington, 5 Jan 1931, E. A. Plank.

Other material examined. 1 ♀ Anderson’s Bay, Dunedin, 10 Nov 1925, Peninsula Co, South Island, C.E. Clarke Collection (AMNZ). Appears to belong to this species, but is omitted from the type series as it is the only specimen from the South Island.

Diagnosis. *R. brevifissas* n. sp. very closely resembles *R. stewartensis* (in head shape, widely spaced punctuation on posterior pronotal lobe and short ovipositor cleft) but is easily distinguished from it by the long, outstanding hairs on all tibiae, the semi-erect hairs on hemelytra, and by the pale second and third antennal segments.

Distribution. Occurs on mountains and at low levels in the southern half of the North Island, and may prove to be more widely distributed.

Biology. As *R. stewartensis* breeds on *Epilobium*, it seems certain that *R. brevifissas*, taken under isolated plants growing on stones beside a creek, also breeds on it.

Remarks. Genitalia and sides of pronotum typical. Some specimens of *R. brevifissas* have, in the past, been confused with *R. clavicornis*, but characters described in the present study show that it is nothing like that species.

Rhyodes brevipilis n. sp.
(Fig. 11, 60, 67–71)



Fig. 60 *Rhyodes brevipilis* n. sp. holotype ♂.

Characterised by the slender femora, shape of pronotum, and short 1st rostral segment.

Colour. Mainly brown; dull except for posterior pronotal lobe. Head black, with a narrow orange stripe on edges of vertex; antennae black or dark brown, with a very narrow pale band at apices of 2nd and 3rd segments. Pronotum black or dark on anterior lobe, brown on posterior lobe. Scutellum black, with obscure mid-longitudinal and lateral orange stripes in apical half. Clavus and corium uniformly brown.

Femora black or dark brown; tibiae light brown, with dark apex and base.

Structure. Size: ♂ – length 5.6–6.0, width 2.2. Form egg-shaped; connexivum partly exposed. Semi-erect hairs on dorsum of head near eyes only; lacking semi-erect hairs on hemelytra and tuft of long hairs laterally at base of costal margin.

Head width to length 1.25 : 1.15. Eye length 1.68 distance between anterior of eye and base of antenna, 0.40 : 0.25. Width of vertex 3× eye width, 0.75 : 0.25; vertex not elevated above eyes; juga prominent. Antennal segments 0.58 : 1.1 : 0.8 : 1.0; 1st segment with half of its length projecting beyond tip of tylus. Head in side view appearing long and narrow. Rostrum reaching hind coxae; 1st segment not reaching base of head.

Pronotum width to length 1.8 : 1.15; sides sinuate, flaring to postero-lateral corners (Fig. 60) not greatly elevated (Fig. 67); punctuation on posterior lobe coarse, dense. Scutellum width to length 1.10 : 0.82; apex acute, upturned. Femora slender (Fig. 68).

Genitalia. Paramere (Fig. 69) with blade short, curved throughout, tapering. Aedeagus (Fig. 70) with very short conjunctiva; vesica with 2 small membranous lobes at base and 1 large membranous lobe (in addition to the ear-like lobes); ejaculatory reservoir (Fig. 71) robust, shorter than usual.

Type data. Holotype ♂ (6.0 × 2.2 mm), MK, Kea Walk, Mt Cook area, on *Hebe subalpina*, 7 Jan 1966, A. C. Eyles (NZAC). Paratype (1 ♂; NZAC): same data as holotype except collected by J. I. Townsend.

Diagnosis. *R. brevipilis* n. sp. is distinguished from *R. rupestris* n. sp. by the slender fore femora, shorter rostrum and first rostral segment, and erect hairs on posterior pronotal lobe.

Distribution. So far known from Mt Cook National Park.

Biology. *Hebe subalpina* may well be the host plant as *R. spadix* n. sp. breeds on it.

Remarks. Closely resembles the next species, *R. bucculentus* n. sp. Paramere typical, but sides of pronotum as in *R. rupestris* n. sp.

Rhyodes bucculentus n. sp.
(Fig. 14, 15, 61, 72–75)

Characterised by the bucculae projecting in front of tylus, slender femora, and shape of pronotum.

Colour. Light brown; dull (Fig. 61). Head black, sometimes with a narrow, yellow band on edges of



61 *Rhyodes bucculentus* n. sp. paratype ♂ (Mt 1).

text; 1st and 4th antennal segments black; 2nd and segments black, with a narrow, bright pale band pex; bucculae with a dark brown band on extreme er edge. Pronotum pale on anterior margin and st of posterior lobe, with brown punctures. itellum with obscure mid-longitudinal orange pe in apical half. Clavus and corium light brown, h many small, pale spots; embolium pale in erior third. Femora dark brown; hind (and netimes mid) femora spotted underneath in basal f; tibiae light brown, dark basally and apically.

ucture. Size: ♂ – length 6.15–6.60, width 2.25–5; ♀ – length 6.80–7.35, width 2.75–3.10. Form g-shaped; connexivum usually broadly exposed both sexes. Semi-erect hairs on dorsum of head r eyes only; lacking semi-erect hairs on hemelytra 1 tuft of long hairs laterally at base of costal rgin.

Head width to length 1.32 : 1.22 (1.42 : 1.27). e length 1.5× distance between anterior of eye d base of antenna, 0.40 : 0.27 (1.35×, 0.4 : 0.3). idth of vertex 2.3× eye width, 0.71 : 0.31 (2.5×,

0.81 : 0.32); vertex lower than level of top of eyes; juga prominent. Antennal segments 0.60 : 1.19 : 0.87 : 0.98 (0.60 : 1.23 : 0.90 : 1.02); 1st segment with about one-third (♀ half) of its length projecting beyond tip of tylus. Head in side view appearing longish and narrow. Bucculae projecting forward beyond tip of tylus (Fig. 72) and longer than width of 1st rostral segment. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.87 : 1.32 (2.30 : 1.42); sides sinuate, flaring to postero-lateral corners not greatly elevated (Fig. 61); punctuation on posterior lobe coarse, dense. Scutellum width to length 1.07 : 0.87 (1.35 : 1.00); apex acute, upturned. Femora slender.

In ♀, abdominal sterna V and VI uncovered in middle; ovipositor cleft less than half as long as abdomen.

Genitalia. Paramere (Fig. 73) rather small, with blade short, curved throughout, tapering, outer edge curled over. Vesica of aedeagus as in Fig. 74; secondary gonopore not flared; ejaculatory reservoir short.

Spermatheca (Fig. 75) with bulb rounded.

Type data. Holotype ♂ (6.15 × 2.55 mm), MC, Mt Hutt, 3800 ft (1160 m), on *Epilobium pycnostachyum* on scree, 12 Dec 1973, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (2 ♂ 4 ♀; NZAC, USNM): 2 ♂ same data as holotype; 1 ♀ MK, Mt Ollivier, 6200 ft (1890 m), Mt Cook National Park, 5 Feb 1977, A. K. Walker; 2 ♀ MB, upper Wairau Valley, Wairau Bridge above Judges Creek, 6 Sep 1966, J. I. Townsend; 1 ♀ Sedgemere, 4000 ft (1220 m), upper Wairau Valley, under stones, 6 Sep 1966, L. P. Marchant.

Diagnosis. *R. bucculentus* n. sp. is similar to *R. brevipilis* n. sp. from which it is easily distinguished by the forward projecting bucculae visible from above, length of bucculae which is greater than width of first rostral segment, and longer first rostral segment.

Distribution. A mountain species in Mackenzie, Canterbury and Marlborough.

Biology. Taken at high altitude on an isolated plant of *Epilobium pycnostachyum* on a scree, a good indication of a true host association, bearing in mind that *R. stewartensis* breeds on *Epilobium*. Shelters under stones.

Remarks. This extraordinary species and *R. brevipilis* n. sp. are somewhat intermediate between *R. rupestris* n. sp. and *R. eminens* n. sp., and *R. clavicornis*, *R. spadix* n. sp. like species.

Rhyodes celmisiae n. sp.
(Fig. 8, 62, 76–81)

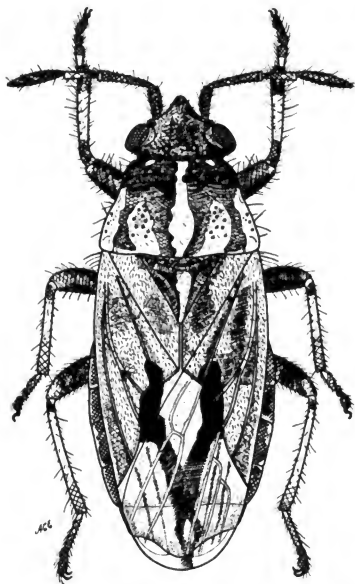


Fig. 62 *Rhyodes celmisiae* n. sp. drawn from holotype ♀.

Characterised by the convex vertex, black rectangles on wings leading to a black X on membrane, and small size.

Colour. Black and fawn; shiny. Head black, with a narrow pale stripe on edges of vertex; antennae black, with apex of 3rd and extreme apex of 2nd segment pale; antenniferous tubercles black throughout; bucculae black or mainly black. Pronotum with 4 longitudinal dark stripes. Scutellum black, with a mid-longitudinal pale stripe almost reaching base. Clavus with variable amount of pale along middle (sometimes dark). Corium fawn, with a broad, diagonal, dark brown stripe near middle,

and an irregular brown stripe following costal margin. A black, longitudinal rectangle over part of corium and membrane on each side leads into a black X on membrane (Fig. 62). Femora black, with a pale spot at apex; tibiae pale, with dark base and apex.

Structure. Size: ♂ – length 4.2–5.1, width 1.50–1.95; ♀ – length 4.6–5.7, width 1.90–2.25. Form oval; macropterous and sub-brachypterous; connexivum broadly or slightly exposed in both sexes (often unexposed). Hemelytra with semi-erect hairs well distributed; fore tibiae with long outstanding hairs; mid tibiae with long and short hairs.

Head width to length 1.15 : 0.95 (1.27 : 1.05). Eye length 1.6× distance between anterior of eye and base of antenna, 0.34 : 0.21 (1.4×, 0.35 : 0.24). Width of vertex 2.7× eye width, 0.68 : 0.25 (3.1×, 0.78 : 0.25); vertex convex above level of top of eyes; juga prominent. Antennal segments 0.37 : 0.67 : 0.51 : 0.72 (0.40 : 0.67 : 0.50 : 0.79); 1st segment with one-third of its length projecting beyond tip of tylus. Head in side view short and thick (Fig. 76). Rostrum reaching hind coxae; 1st segment reaching base of head.

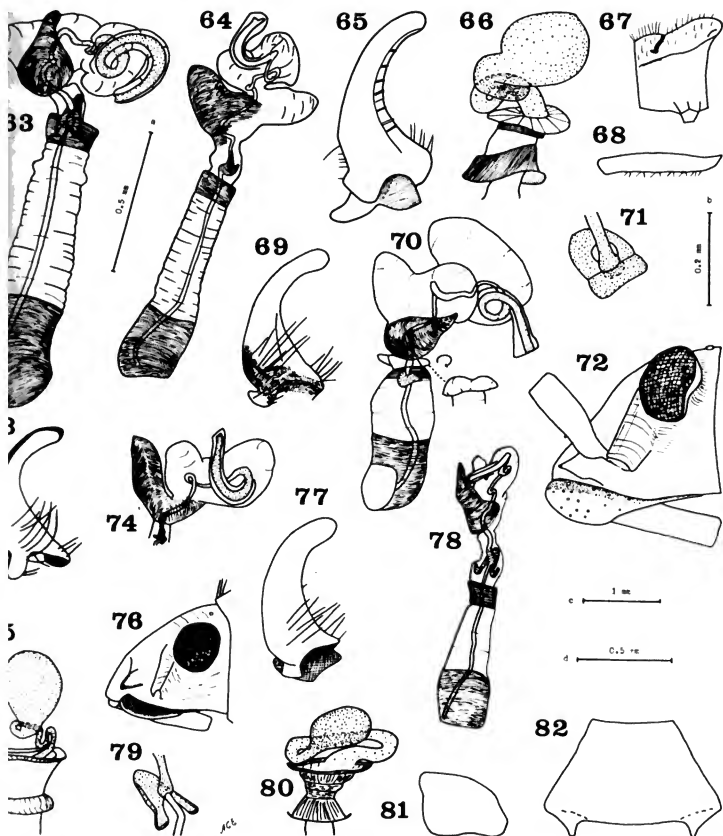
Pronotum width to length 1.63 : 1.01 (1.83 : 1.12); sides gently sinuate, not suddenly tapering anteriorly; punctuation on posterior lobe coarse, widely spaced. Scutellum width to length 0.87 : 0.68 (1.14 : 0.85); apex acute, level. Membrane with 1A joining PCu (Fig. 8).

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 77) with blade short, curved throughout, tapering. Aedeagus as in Fig. 78; ejaculatory reservoir (Fig. 79) with large wings, curled at edges.

Spermatheca (Fig. 80) with bulb short, but lying over. Ring sclerites small (Fig. 81).

Type data. Holotype ♀ (5.0×2.0mm), OL, Coronet Peak, top, 4500 ft (1372 m), on *Celmisia*, 2 Dec 1963, J. I. Townsend (NZAC). Allotype ♂ CO, Old Man Range, 4500 ft, on *Celmisia prorrepens*, 16 Jan 1965, G. Kuschel and J. I. T. (NZAC). Paratypes (16 ♂ 15 ♀; BMNH, FRNZ, NZAC, USNM): 3 ♀ same data as holotype; 1 ♂ 1 ♀ Coronet Peak, 1520 m, sweeping, 14 Feb 1976, L. L. Deitz; 1 ♂ 1 ♀ same data as allotype; 1 ♀ Old Man Range, 1616 m, on *Celmisia*, 20 Feb 1974, R. R. Forster; 1 ♂ Old Man Range near top, Vincent Lake, on *Gentiana bellidifolia*, 22 Feb 1973, B. J. Donovan; 1 ♂ Old Man Range, Shingle Creek, 6 Dec 1963, J. S. Dugdale.



63-82 63, *R. brachypterus* n. sp. aedeagus of paratype ♂; 64-66 *R. brevifissus* n. sp.: 64, aedeagus; 65, left paramere of paratype ♂ Ohakune; 66, spermatheca of paratype ♀ (Tarawera); 67-71 *R. brevipilis* n. sp.: 67, prothorax, side view; 68, left fore femur, posterior aspect (both of paratype ♂); 69, left paramere; 70, aedeagus; 71, ejaculatory reservoir of holotype ♂; 72-75 *R. bucculentus* n. sp.: 72, head, side view of paratype ♀ (Upper Wairau Vly); 73, left paramere; 74, vesica of aedeagus (both of paratype ♂ Mt Hutt); 75, spermatheca of allotype ♀; 76-81 *R. celmisiae* n. sp.: 76, head, side view of paratype ♂ (Rock and Pillar Ra.); 77, left paramere; 78, aedeagus (both of allotype ♂); 79, ejaculatory reservoir of paratype ♂ (Mt Arthur); 80, spermatheca; 81, ring sclerite (both of paratype ♀ Coronet Peak); 82, *R. clavicornis*, notum of ♀ (Mt Tongariro). Fig. 63 to scale a; 65, 66, 69, 71, 73, 75, 77, 79, 80, 81 to scale b; 64, 74, 78, to half scale b; 67, 68, 82 to scale c; 72 to scale d.

FRI 43; 1 ♂ 1 ♀ CO, Rock and Pillar Range, 4000–4700 ft, sweeping, 11 Nov 1969, J.S.D.; 2 ♂ 4 ♀ NN, Mt Arthur, 1767 m (5800 ft), on green *Raoulia* mat plants, 23 Mar 1971, A. C. Eyles; 7 ♂ 3 ♀ Mt Arthur, 1680 m, 19 Nov 1969, J.I.T.; 1 ♂ 1 ♀ Mt Arthur, 3500 ft (1067 m), 13–16 Dec 1961, J.I.T. and G. F. Woods; 1 ♂ Mt Arthur, 21 Dec 1920, T. Cockcroft.

Other material examined. 50 specimens, all NZAC: one 5th instar nymph on *Celmisia prorepens*, same data as allotype; 28, CO, Pisa Range, 1508 m, on grass swards by creek, also under stones and cushion plants, and at 1700 m, Lake Mackay, J. S. Dugdale and J. C. Watt; 12, CO, Dunstan Range, 1560 m, some on mat plants, J.S.D.; 1, CO, Old Woman Range, summit, 1396 m, on grass, J.S.D.; 2 + 1 nymph, CO, Mt Bitterness, in litter, J.S.D.; 1, FD, W. Olivine Range, Simonin Pass, J.S.D.; 3, NN, Mt Peel, 5500 ft (1677 m), A. Philpott; 1, NN, Mt Robert, on mat plants, J. McBurney.

Diagnosis. *R. celmisiae* n. sp. is probably closest to *R. myersi*, but is readily distinguished from it and all other species of *Rhyodes* by the small size and distinctive wing markings.

Distribution. A mountain species taken in Nelson, Central Otago, Otago lakes and Fiordland, which suggests that it may be spread throughout mountain ranges of the South Island.

Biology. Breeds on *Celmisia prorepens* as adults and a fifth instar nymph were taken on this plant. Probably breeds on other species of *Celmisia*. It may also feed on other plants as it has been taken on grass swards (in large numbers), *Raoulia* mats, *Gentiana bellidifolia*, and sheltering under stones. This species and *R. longiceps* n. sp. were found at higher levels and the summit of Coronet Peak, whereas *R. myersi* was found on the lower slopes.

Remarks. Sides of pronotum and genitalia are more or less typical. This is the smallest species in the genus, one male measuring 3.80×1.45 mm. Although some *R. anceps* are smaller than this, probably because of brachyptery, the largest specimens of *anceps* are larger than those of *R. celmisiae*. Some of the non-type specimens have alternate brown and fawn (or clear) stripes on the membrane.

Rhyodes chinai Usinger
(Fig. 83, 84, 89–93)

Rhyodes chinai Usinger 1942b: 49–51 (Original description; keyed).



Fig. 83 *Rhyodes chinai* Usinger ♀ (Mt Matthews).



Fig. 84 Distribution of *Rhyodes chinai* Usinger.

ypodes chinai: Slater 1964: 344 (Catalogue).

ypodes chinai: Ashlock 1967: 56 (List).

ypodes chinai: White 1969: 21–22 (Host plant; biology notes; egg description).

ypodes chinai: Wise 1977: 122 (List).

characterised by the pale subapical corial spot (Fig. 1), triangular plate-like projections on posterior margin of pronotum, prominent head hairs near eyes, and shape of paramere.

Colour. Pale, with some black; shiny. Head black; antennae black except for a pale band at apex of 3rd segment; antenniferous tubercles black throughout. Pronotum mostly pale, with a brown spot near posterior corners; some specimens with a longitudinal brown stripe each side of middle. Scutellum black, with a mid-longitudinal pale stripe in apical half. Abdomen mostly pale except for a tapering brown streak on inner part of basal third. Corium mostly pale, with pale subapical spot brighter; apex and a few blotches cross middle, brown. Femora black or dark brown, with pale yellow or orange apex; hind femora pale at base; hind and sometimes mid femora with black spots; tibiae pale, with a dark band at apex and base.

Structure. Size: ♂ – length 5.0–6.0, width 1.70–1.05; ♀ – length 5.3–6.3, width 1.85–2.30. Form oval; body flattened; connexivum usually unexposed slightly exposed in some ♀). Semi-erect hairs on pronotum of head near eyes only; lacking semi-erect hairs on hemelytra.

Head width to length 1.15 : 1.03 (1.18 : 1.07). Eye length 1.73× distance between anterior of eye and base of antenna, 0.38 : 0.22 (1.5×, 0.36 : 0.24). Width of vertex 2.45× eye width, 0.64 : 0.26 (2.8×, 1.70 : 0.25); vertex not elevated above eyes; jugal prominent. Antennal segments 0.38 : 0.84 : 0.53 : 1.64 (0.36 : 0.80 : 0.54 : 0.67); 1st segment with about one-third (♀ one-fourth) of its length projecting beyond tip of tylus. Head in side view appearing long and narrow. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.67 : 1.04 (1.82 : 1.14); sides straightish (in ♂ slightly sinuate), not suddenly tapering anteriorly; posterior margin with 2 large, triangular, plate-like projections overlapping bases of clavi (Fig. 89); punctation on posterior lobe coarse, widely spaced. Scutellum width to length 1.94 : 0.75 (1.07 : 0.81); apex acute, level.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft usually more than half as long as abdomen.

Genitalia. Paramere (Fig. 90) with blade shortish, horn-shaped, bearing small, tooth-like spines.

Aedeagus (Fig. 91) with small lobe on vesica before sclerotised lobe; ejaculatory reservoir broad.

Spermatheca (Fig. 92) with bulbelongate, narrow, lying over; flange with upper lip wide, flat. Ring sclerites (Fig. 93) larger than spermathecal bulb.

Material examined. 3 ♂ paratypes, WN, Mt Matthews, 3000 ft (915 m), 25 Sep 1921 (= same data as holotype) (CASC). 3 ♂ 3 ♀ not paratypes, but same data as holotype (NZAC). Plus 273 specimens (AMNZ, CMNZ, FRNZ, NMNZ, NZAC).

Diagnosis. *R. chinai* is distinguished from *R. clavicornis* by the pale subapical corial spot, and from *R. triangulus* n. sp. by the pale, rather than yellow, wings and antennal banding, spines on the parameres, and sterna V and VI on the female abdomen covered in middle.

Distribution. Although the type locality is Mt Matthews in the Rimutaka Range, this species has not been taken north of the vicinity of Wellington (Orongorongo Valley), but occurs throughout the South Island (Fig. 84). The only South Island areas from which specimens have not been seen are Dunedin and Southland. This is a lowland and mountain species, taken from sea level to 6500 ft (1982 m).

Biology. Breeds on *Raoulia* and probably *Celmisia* species. Taken on *Raoulia tenuicaulis*, *Raoulia australis*, *Raoulia haastii*, *Celmisia semicordata* subsp. *semicordata*, *Celmisia spectabilis* subsp. *spectabilis*, *Aciphylla*, *Dolichoglottis scorzonoides*, *Cassinia*, *Muehlenbeckia*, *Chionochloa*, *Haastia pulvinaris*, *Olearia virgata*, and tussock. Further information has been given in the biology section and Tables 3 and 4.

Remarks. The holotype male (BMNH) was not seen. Pronotum and genitalia typical. There is considerable variation in this species. Some specimens (particularly males) are narrower, with a velvety, purplish appearance, whereas others seem broader and more brown. One-third of specimens (in both islands) lack pronotal triangles. The material may contain more than one species, but if so, the writer was unable to separate them. Of all the species of *Rhyodes*, this species superficially looks like *Nysius*, and in collections many specimens of *R. chinai* had been placed under *Nysius huttoni*.

Rhyodes clavicornis (Fabricius)

(Fig. 7, 19, 22, 24, 27, 28, 33, 82, 85, 86, 94–96)

Lygaeus clavicornis Fabricius 1794: 169 (Original description).



Fig. 85 *Rhypodes clavicornis* (Fabricius): lectotype ♀ of *Nysius zealandicus* Dallas, the type of the genus.

Nysius zealandicus Dallas 1852: 552 (Description; synonym; syn. by Stål 1868).

Nysius (*Rhypodes*) *zealandicus*: Stål 1868: 76 (As type *Rhypodes* new subgenus; synonym).

Nysius clavicornis: Myers 1926: 479–480 (Biology notes).

Myersia clavicornis: Evans 1929a: 353 (New genus). *Rhypodes clavicornis*: Evans 1929b: 269 (Sinks *Myersia* as synonym).

Rhypodes clavicornis: Usinger 1942b: 45–46 (Keyed; notes).

Rhypodes clavicornis: Woodward 1954: 216, 222–223 (On Three Kings Is; variation; host plants).

Nysius zealandicus: Opinion 319 1955: (Fixed as type *Rhypodes*; on official list specific names).

Rhypodes clavicornis: Slater 1964: 344–345 (Catalogue).

Rhypodes clavicornis: Ashlock 1967: 56 (Figs including genitalia).

Rhypodes clavicornis: Eyles 1974: 954–956 (Host plants; distinction; Fig.).

Rhypodes clavicornis: Wise 1977: 122 (List).

Rhypodes clavicornis: Ueshima & Ashlock 1980: 731, 733–734, 793 (Chromosomes including figures).

Characterised by the triangular, plate-like projections on posterior margin of pronotum, absence of a pale subapical corial spot, and rather narrow, parallel-sided males.

Colour. Mostly brown, with hemelytra sometimes variegated (Fig. 85); shiny. Head black; antennae dark brown; 1st segment pale at base; 2nd segment with a narrow pale band at apex; 3rd segment with a wider pale band at apex (sometimes pale in apical half). Scutellum with a mid-longitudinal pale stripe in apical half (sometimes mostly pale). Clavus and corium with some darker brown blotches; sometimes variegated with variable amount of small, round, pale spots. Femora pale, with brown spots; tibiae pale, with dark apex and a brown band near base.

Structure. Size: ♂ – length 5.4–6.5, width 1.7–2.2; ♀ – length 6.0–7.0, width 2.05–2.85. Form oval; males rather narrow, with wings almost parallel sided, but pronotum at posterior considerably wider than head; connexivum partly (occasionally broadly) exposed in some ♀, unexposed in ♂. Hemelytra with semi-erect hairs well distributed.

Head width to length 1.28 : 1.03 (1.36 : 1.12). Eye length 2.1× distance between anterior of eye and base of antenna, 0.40 : 0.19 (1.9×, 0.42 : 0.22). Width of vertex 2.4× eye width, 0.69 : 0.29 (2.55×, 0.76 : 0.30); vertex not elevated above eyes; jugs prominent. Antennal segments 0.39 : 0.92 0.74 : 0.86 (0.40 : 0.98 : 0.79 : 0.93); 1st segment with one-third (♀ three-eighths) of its length projecting beyond tip of tylus. Head in side view short and thick (Fig. 94). Rostrum reaching mid coxae; 1st segment reaching slightly beyond base of head.

Pronotum width to length 1.84 : 1.22 (2.12 : 1.34); sides straightish, not suddenly tapering anteriorly; posterior margin with 2 large, triangular, plate-like projections overlapping bases of clavi (Fig. 82); punctuation on posterior lobe coarse, dense. Scutellum width to length 1.09 : 0.77 (1.24 : 0.94); apex rounded, upturned.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft less than half as long as abdomen (Fig. 33).

Genitalia. Paramere (Fig. 95) with blade short, curved throughout, tapering. Aedeagus (Fig. 96) with membranous lobe near apex of conjunctiva; apical part of seminal duct ensheathed in membrane; secondary gonopore flared; ejaculatory reservoir (Fig. 28) with broad, triangular wings.



Fig. 86 Distribution of *Rhypodes clavicornis* (Fabricius).

Spermatheca (Fig. 27) with bulb elongate, lying over.

Material examined. Holotype ♂ (6.1 × 2.1 mm) of *Lygaeus clavicornis* Fabricius (Universitets Zoologiske Museum, Copenhagen), with labels "♂" and "Nova Zealandia, Stål, Zealandicus Dall." in Stål's handwriting. I have added labels "Holotype ♂, *Lygaeus clavicornis* Fabricius 1794, Det. A. C. Eyles 1970" and "*Rhypodes clavicornis* (Fabricius, 1794), Det. A. C. Eyles 1970." Lectotype ♀ (7.0 × 1.55 mm) of *Nysius zealandicus* Dallas (BMNH) with labels "New Zealand" written in ink and on the other side "45, 61", circular B.M. "Type" label with orange border, and "35 *Nysius Zealandicus*", a printed cutout from a paper or list. As Dallas had more than one specimen before him and did not designate a holotype, this specimen is hereby designated lectotype of *Nysius zealandicus* and labelled as such. Plus 170 specimens (FRNZ, GGES, TFPM, NMNZ, NZAC).

Diagnosis. *R. clavicornis* is distinguished from most species of *Rhypodes* by the large, triangular, plate-

like projections on posterior margin of pronotum, and from *R. chinai* and *R. triangulus* n. sp. by the absence of a pale subapical corial spot.

Distribution. A lowland and mountain species taken in numbers from sea level to 3700 ft (1130 m), but also taken at 6200 ft (1890 m). This abundant species occurs throughout the North Island, but in the South Island has been taken only at Nelson, Puponga, Waiho Gorge (near Franz Josef), and Bluff (Fig. 86). It has been taken on the Three Kings Islands (Woodward 1954), in all areas of the North Island (at several localities in all but two of those areas), Cavalli Island off the Northland east coast, and Little Barrier Island, the Aldermen Islands and Mayor Island off the Coromandel coast.

Biology. It breeds at low, medium, and high levels as nymphs have been taken at those levels. Breeds on several species of Compositae—*Celmisia*, *Senecio*, *Cassinia*, *Eupatorium*; Myoporaceae—*Myoporum*; Myrtaceae—*Leptospermum*, and has also been taken on weeds, grasses, rushes, and sedges (see biology section, Tables 3 and 4 and Woodward 1954).

Remarks. As the locality published for the type of *R. clavicornis* is in error—the specimen was only labelled "Selandia" (Stål 1868; Evans 1929b; Usinger 1942b; Slater 1964)—and as the type for *Nysius zealandicus* was from "New Zealand", there is no official type locality. Therefore, the Rimutaka Range, Wellington is hereby designated type locality for *R. clavicornis*.

The pronotal triangular projections, with pointed apices (usually longish points) are so distinctive and universal in North Island specimens, that the species is herein limited to those specimens which have them. The types of both Fabricius and Dallas have them. *R. clavicornis* with triangles occurs in the South Island. One of the specimens from Nelson has a triangle on one side, but not the other. The material which Usinger (1942b) included in *R. clavicornis* contained more than one species (see remarks under *R. cognatus* n. sp. and *R. koebelei* n. sp.).

A series of specimens from Stephen's Island, Ship Cove, Nelson, other parts of the South Island, and Codfish Island (off Stewart Island) lacking the triangles, but otherwise closely resembling *clavicornis*, have been assigned to a new species, *R. cognatus* (see below).

The variation in *clavicornis* from the Three Kings Islands outlined by Woodward (1954) has not been followed up because insufficient material was available and Woodward's material (held at Queensland University) was not on hand for comparison. The problem calls for a detailed study on all the islands of the group. Also, it needs to be determined if other members of the genus occur there. It is hoped that the present study, in establishing what true *clavicornis* is, will help in resolving this interesting problem.

***Rhyodes cognatus* n. sp.**
(Fig. 87, 97–99)

Characterised by the coarse, dense punctation on posterior pronotal lobe, rather narrow, parallel sided males, and absence of triangular, plate-like projections on posterior margin of pronotum.

Colour (Fig. 87). Brown; shiny. Head black; antennae black; 1st segment pale at base; 2nd and 3rd segments with a pale band at apex (narrower on 2nd segment; sometimes 3rd segment with up to apical half lighter brown). Scutellum with a mid-longitudinal pale stripe in apical half (sometimes mostly pale). Clavus and corium lightly variegated with varying amount of small, pale spots on brown. Femora pale, with



Fig. 87 *Rhyodes cognatus* n. sp. paratype ♀ (Stephens I).

dark spots; tibiae pale, with a dark band at apex and near base.

Structure. Size: ♂ – length 4.9–5.8, width 1.64–2.00; ♀ – length 4.9–6.6, width 1.9–2.4. Form oval; males rather narrow, with wings almost parallel sided, but pronotum at posterior considerably wider than head; connexivum usually partly (occasionally broadly) exposed in ♀, usually unexposed in ♂. Hemelytra with semi-erect hairs well distributed.

Head width to length 1.14 : 0.87 (1.20 : 0.94). Eye length 2.15× distance between anterior of eye and base of antenna, 0.34 : 0.16 (1.85×, 0.35 : 0.19). Width of vertex 2.95× eye width, 0.68 : 0.23 (3.45×, 0.76 : 0.22); vertex not elevated above eyes; jugae prominent. Antennal segments 0.37 : 0.79 : 0.61 : 0.73 (0.38 : 0.84 : 0.67 : 0.81); 1st segment with one-third of its length projecting beyond tip of tylus. Head in side view short and thick. Rostrum reaching mid coxae; 1st segment reaching base of head.

Pronotum width to length 1.62 : 1.03 (1.84 : 1.10); sides straightish, not suddenly tapering

anteriorly; punctation on posterior lobe coarse, dense. Scutellum width to length 0.96 : 0.74 (1.09 : 0.82); pex rounded, upturned.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft less than half as long as abdomen.

Genitalia. Paramere (Fig. 98) with blade short, curved throughout, tapering. Aedeagus as in Fig. 97.

Spermatheca (Fig. 99) with bulb elongate, lying over; duct with double kink near flange.

Type data. Holotype ♂ (5.50 × 1.78 mm), SD, Shipcove, sweeping grass and weeds, 15 Feb 1973, A. C. Eyles (NZAC). Allotype ♀ some data as holotype (NZAC). Paratypes (33 ♂ 37 ♀; BMNH, NMNZ, NZAC, USNM): 2 ♂ 2 ♀ same data as holotype; 1 ♀ same data except 27–30 Jan 1972, G. Kuschel; Stephen's Island: 1 ♂ 1 ♀ 1972, R. J. Gillyard; 3 ♂ 9 Feb 1964, J. R. McMillan; 2 ♂ 4 ♀ 19 Feb 1964, J. I. Townsend; 2 ♂ on *Cassinia leptophylla*, Feb 1971, G. Kuschel; 1 ♂ sweeping, Feb 1971, J. McBurney; 5 ♂ 8 ♀ sweeping tussock, Feb 1971, G. W. Ramsay; 1 ♀ 1 Dec 1953, B. A. Holloway; Inner Chetwode Island: 1 ♂ 12 Nov 1961, B. A. H.; The Brothers: 2 ♂ 1 ♀ on *Senecio*, 7 Oct 1954, R. Ordish; NN, Nelson: 2 ♂ 5 ♀ on sow thistle, 5 Nov 1962, A. K. Walker; 1 ♀ sweeping grass and weeds, 9 Dec 1965, A. C. E.; 1 ♂ Dec 1951, A. W. Parrott; 1 ♀ 23 Dec 1965, E. S. Gourlay; 1 ♀ 27 Mar 1971, E. S. G.; 1 ♀ roadside, 14 Dec 1965, E. S. G.; 1 ♀ Botanical Hill, on flowering *Brachyglottis repanda*, 26 Sep 1967, J. C. Watt; 2 ♂ 8 Jan 1942, No. 629, labelled "*Nysius clavicornis*"; SI, Codfish Island: 9 ♂ 8 ♀ rocky islet off E end of Stephen's Bay, on *Olearia angustifolia* flowers, 13 Dec 1966, J. I. Townsend; 1 ♂ 1 ♀ in sand dunes behind Sealer's Bay, 13 Dec 1966, J. I. T.

Other material examined. 108 specimens (CMNZ, FRNZ, NZAC).

Diagnosis. *R. cognatus* n. sp. closely resembles *R. clavicornis* even to the narrower, more parallel sided males, but is easily distinguished from it by the absence of large, triangular, plate-like projections on posterior margin of pronotum. *R. cognatus* is distinguished from *R. spadicus* n. sp. by the shorter rostrum, reaching only to mid coxae.

Distribution. Mainly a lowland species, but has been taken at 600 m on Mt Dun and 1300 m on Fell Peak. Occurs throughout the South Island (the only areas where it has not been taken being Kaikoura, Mackenzie, Dunedin and N and S Canterbury) and on Stewart Island.

Biology. Taken in large numbers sweeping tussock on Stephen's Island and on *Olearia angustifolia* on

Codfish Island. It has also been taken on *Cassinia leptophylla*, *Senecio jacobaea*, *Olearia virgata* (with nymphs), *Sonchus oleraceus*, *Brachyglottis repanda*, lucerne, grass, and weeds. Females taken on sow thistle laid eggs in the cotton wool plug and not on the sow thistle flowers provided.

Remarks. Genitalia and sides of pronotum typical. Usinger (1942b) no doubt intended the form with narrower males (= *cognatus*) when he stated that pronotal triangles may not be a specific character. The other species he described are markedly different from *clavicornis*. However, many of the new species described herein are nearer in form to *clavicornis* than to *myersi* and *chinai*, but do not have pronotal triangles and do not have noticeably narrower males. It is unfortunate that until now, through lack of knowledge of the group, Usinger's statement had led to some confusion and a tendency to lump everything lacking triangles in with *clavicornis*. Although not possessing pronotal triangles, *R. cognatus* n. sp. has very short, rounded, insignificant extensions in the same place.

R. cognatus has been separated from *clavicornis* because:

- 1 A situation where practically all the specimens in the South Island, but none in the North Island, lack pronotal triangles, seems wrong.
- 2 *R. clavicornis* with well developed triangles occurs in the South Island.
- 3 There appeared to be a behavioural difference in oviposition site, in captivity.
- 4 It is necessary to describe the two forms, as any attempt to determine the status of *cognatus* depends on knowing what true *clavicornis* is, and what *cognatus* is (in view of the many similar species without triangles).

Rypodes crinitus n. sp.

(Fig. 88)

Characterised by the covering of very long, outstanding hairs, particularly on hemelytra and all tibiae, the mainly black antennae, widely spaced pronotal punctures, and pale basal half of embolium.

Colour. Mostly brown; shiny. Head black. Antennae black, with the following pale areas: extreme apices of first 3 segments and extreme base of 1st segment. Scutellum with mid-longitudinal and lateral pale stripes in apical half. Embolium pale at least in basal half (Fig. 88). Femora dark brown, with a pale spot at apex; mid and hind femora spotted underneath in basal half; tibiae pale except apically and basally.



Fig. 88 *Rhypodes crinitus* n. sp. allotype ♂.

Structure. Size: ♂ – length 5.57, width 2.0; ♀ – length 5.6, width 2.3. Form oval; connexivum slightly exposed in ♀, unexposed in ♂. Covered with very long, outstanding hairs, particularly on hemelytra and all tibiae.

Head width to length 1.33 : 1.06 (1.36 : 1.10). Eye length 1.85–1.9× distance between anterior of eye and base of antenna, 0.36 : 0.19 (0.37 : 0.20). Width of vertex 2.95× eye width, 0.80 : 0.27 (2.8×, 0.80 : 0.28); vertex scarcely elevated above level of top of eyes; jugal prominent. Antennal segments 0.40 : 0.85 : 0.64 : 0.82 (0.45 : 0.9 : 0.7 : 1.0); 1st segment with three-eighths (♀ about one-fifth) of its length projecting beyond tip of tylus. Head in side view appearing relatively short and thick. Rostrum reaching slightly beyond hind coxae; 1st segment reaching beyond base of head.

Pronotum width to length 1.88 : 1.34 (2.00 : 1.25); sides straightish, not suddenly tapering

anteriorly; punctation on posterior lobe coarse, widely spaced. Scutellum width to length 1.03 : 0.84 (1.15 : 0.90); apex acute, level. Membrane with 1A joining PCu (as in Fig. 8).

In ♀, abdominal sternum VI covered in middle; ovipositor cleft about half as long as abdomen.

Type data. Holotype ♀ BP, GB boundary, Mount Maungapohatu, 1036–1112 m, sweeping grass and *Carex solandri*, 3 Mar 1971, A. C. Eyles (NZAC); taken as 5th instar nymph (exuvium with type). Allotype ♂ same data as holotype except taken as adult (NZAC). Paratype: 1 ♀ RI, Ruahine Range, 3000–4000 ft (915–1220 m), Oct 1983, P. Thurston (TFPM).

Diagnosis. *R. crinitus* n. sp. is distinguished from *R. brevifissas* n. sp. by the longer rostrum and first rostral segment, longer ovipositor cleft, wider embolium, and longer erect hairs on hemelytra.

Distribution. So far known from Urewera National Park and Ruahine Range.

Biology. Probably feeds on *Carex solandri* as an adult and fifth instar nymph were swept from the seedheads. The nymph, provided with *Carex* seeds, later moulted.

Remarks. Sides of pronotum typical.

Rhypodes depilis n. sp. (Fig. 100, 101, 109–111)

Characterised by the flat, unelevated pronotum, with long, erect hairs on anterior margin only, and by the large size.

Colour (Fig. 101). Mostly pale straw coloured, with some black; shiny. Head black; 1st and 4th antennal segments black; 2nd and 3rd segments black, with a narrow pale band at apex; antenniferous tubercles black throughout. Pronotum with a narrow, black band in front of calli; posterior lobe pale, with brown spot near posterior corners. Scutellum black with a mid-longitudinal pale stripe in apical half. Clavus and corium straw coloured, with a few small brown marks and small, round, pale spots; apical angle of corium dark brown. Femora mostly dark, with a pale spot at apex; hind femora (and mid femora obscurely) with some brown spotting underneath in basal half; tibiae orange, with brown apex and base.

Structure. Size: ♂ – length 7.0–7.5, width 2.25–2.50; ♀ – length 7.2–8.3, width 2.3–2.9. Form elongate oval; connexivum partly exposed in both sexes. Spiracle VII in outer sixth of connexivum. Lacking erect or semi-erect hairs except on head

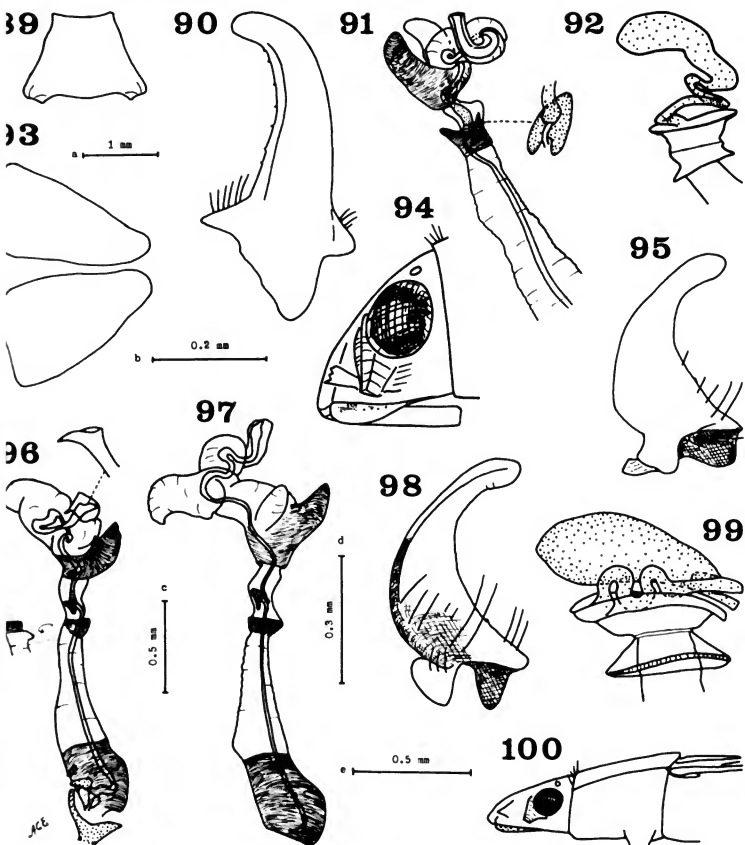


Fig. 89-100 89-93 *R. chinai*: 89, pronotum ♂ (Crown Ra.); 90, right paramere ♂ (Kowhai River); 91, aedeagus ♂ (Sealy Lake); 92, spermatheca; 93, ring sclerites (both ♀ Crown Ra.); 94-96 *R. clavicornis*: 94, head, side view ♂ Rimutakas; 95, left paramere ♂ (Coromandel); 96, aedeagus ♂ (Rimutakas); 97-99 *R. cognatus* n. sp.: 97, aedeagus; 98, left paramere (both of paratype ♂ Ship Cove); 99, spermatheca of paratype ♀ (Nelson); 100, *R. depilis* n. sp. head, part thorax, side view of holotype ♂. Fig. 89, 100 to scale a; 90, 92, 93, 99 to scale b; 91 to half scale b; 94, 96 to scale c; 95, 98 to scale d; 97 to scale e.



Fig. 101 *Rhypodes depilis* n. sp. paratype ♂ (Takahe V).

near eyes only, on pronotum on anterior margin only, and laterally at base of costal margin.

Head width to length 1.39 : 1.24 (1.5 : 1.3). Eye length 1.5× distance between anterior of eye and base of antenna, 0.43 : 0.29 (1.4×, 0.45 : 0.32). Width of vertex 2.9× eye width, 0.81 : 0.28 (3.1×, 0.93 : 0.30); vertex convex above eyes; juga prominent. Antennal segments 0.46 : 1.01 : 0.78 : 0.92 (0.50 : 1.08 : 0.88 : 1.02); 1st segment with one-fourth to one-fifth of its length projecting beyond tip of tylus. Head in side view (Fig. 100) appearing long and narrow. Rostrum reaching beyond hind coxae; 1st segment reaching base of head.

Pronotum width to length 2.08 : 1.30 (2.30 : 1.43); sides gently sinuate, not suddenly tapering anteriorly; disc flat (Fig. 100); punctation on posterior lobe coarse, widely spaced. Scutellum width to length 1.08 : 0.89 (1.33 : 1.03); apex rounded, upturned.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 109) with blade short, curved throughout, tapering, black on outer half.

Aedeagus (Fig. 110) with membranous lobe near apex of conjunctiva; vesica with small lobes before the sclerotised lobe; ejaculatory reservoir with wings more or less triangular.

Spermatheca (Fig. 111) with bulb rounded or lemon-shaped, standing upright; flange with upper lip flat.

Type data. Holotype ♂ (7.35 × 2.35 mm), FD, Takahe Valley, near head Basin, on *Celmisia coriacea*, 11 Dec 1972, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (7 ♂ 4 ♀; BMNH, NZAC, USNM): 3 ♂ 1 ♀ same data as holotype; 1 ♂ Mt Barber, 3000–4350 ft (915–1325 m), Wilmot Pass, 15 Jan 1970, J. S. Dugdale; 1 ♀ above Homer Tunnel, 4300 ft, general beating, 13 Jan 1967, A. K. Walker; 1 ♂ 1 ♀ Mackinnon Pass, 3600 ft (1100 m), ex *Senecio*, 1 Jan 1963, B. M. May; 1 ♂ W Olivine Range, Tempest Spur, 1220–1340 m, sweeping tussock, 13 Jan 1975, G. W. Ramsay; 1 ♀ W Olivine Range, Simonin Pass, 975 m, 23 Jan–4 Feb 1975, J. S. D.; 1 ♂ Darran Mts, Middle Gully, Tutoko Bench, 945–1190 m, 13 Jan 1977, J. S. Dugdale.

Diagnosis. *R. depilis* n. sp. is readily distinguished from *R. atricornis* n. sp. by the flat unelevated pronotum, absence of long erect hairs on pronotum except for anterior margin, and by the longer rostrum and first rostral segment.

Distribution. Fiordland National Park at high altitude.

Biology. Several adults were taken on *Celmisia coriacea*, and two on *Senecio*.

Remarks. Typical for male genitalia and more or less for sides of pronotum, but female genitalia as in *R. rupestris*.

***Rhypodes eminens* n. sp.**
(Fig. 16, 17, 26, 102, 105–108)

Characterised by the mound on the head.

Colour. Dull, grey. 1st and 4th antennal segments black; 2nd and 3rd segments orange, with dark base and apex (3rd sometimes mostly dark); rostrum dark. Pronotum with 2 broad, longitudinal pale stripes on posterior lobe. Corium with a few small, round, pale spots. Femora dark, with a pale spot at apex; hind femora spotted underneath in basal half; tibiae brownish orange, with a dark band at apex and near base.

Structure. Size: ♂ – length 5.51–5.83, width 1.99–2.14; ♀ – length 5.45–6.07, width 2.14–2.54. Form



fig. 102 *Rhypodes eminens* n. sp. allotype ♀.

egg-shaped; body flattened; connexivum broadly exposed in both sexes. Lacking long, erect, or semi-erect hairs except on anterior lobe of pronotum; pubescence very short.

Head width to length 1.26 : 1.18 (1.31 : 1.20). Base of antenna remote from eye; eye length 0.87× distance between anterior of eye and base of antenna, 0.33 : 0.38 (0.35 : 0.40). Width of vertex 3.2× eye width, 0.77 : 0.24 (3.3×, 0.80 : 0.24); centre of dorsum of head extremely elevated in a mound (Fig. 105); clypeus not prominent. Antennal segments 0.61 : 1.05 : 0.76 : 0.72 (0.62 : 1.03 : 0.75 : 0.71); 1st segment curved at base, slender, with half of its length projecting beyond tip of tylus. Rostrum reaching beyond hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.73 : 1.17 (1.84 : 1.18); sides sinuate, flaring to well developed, elevated posterolateral corners (Fig. 102 and as in Fig. 153); punctuation on posterior lobe shallow, dense. Scutellum width to length 1.00 : 0.78 (1.15 :

1.02); triradiate ridge prominent; apex rounded, prominently upturned.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft more than half as long as abdomen.

Genitalia. Paramere (Fig. 106) with blade long, broad, straight for part of its length, not tapering. Aedeagus (Fig. 107) with 2 sclerotised lobes on vesica (2nd sclerotised on underside); ejaculatory reservoir A-shaped.

Spermatheca (Fig. 108) with bulb lemon-shaped; flange with upper lip upright, sides slightly sloping outwards like a cup.

Type data. Holotype ♂ (5.55 × 2.12 mm), KA, Mt Percival, 5000 ft (1524 m), on *Helichrysum coralloides*, 29 Oct 1962, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC).

Paratypes (BMNH, NZAC, USNM): 6 ♂ 3 ♀ same data as holotype; 1 ♀ Mt St Patrick, 4000 ft (1220 m), on *Helichrysum selago*, 30 Oct 1962, A. C. Eyles.

Diagnosis. *R. eminens* n. sp. is similar to *R. rupestris* n. sp. but is easily distinguished from it and all other known species of *Rhypodes* by the elevated mound on the head, the great distance between anterior of eye and base of antenna compared with eye length, and by the longer first antennal segment (except for *R. bucculentus* n. sp.).

Distribution. So far known from high up on the slopes of the Kaikoura Ranges.

Biology. Host plants *Helichrysum coralloides* and *Helichrysum selago*.

Remarks. This bizarre species and *R. rupestris* n. sp., although different from all other species of *Rhypodes* in the very short pubescence and elevation of the pronotum, cannot be separated from the genus because they share one character (markedly sinuate sided pronotum) with *R. brevipilis* n. sp. and *R. bucculentus* n. sp., and another character (paramere and spermatheca shape) with *R. sericatus* and *R. argenteus* n. sp.

Rhypodes gracilis n. sp. (Fig. 10, 13, 103, 112–116)

Characterised by the slender body (Fig. 103), greyish colour, wide, longitudinal, pale wing stripe, and shape of parameres and spermatheca.

Colour. Mostly brown or greyish brown, with pale wing stripe; shiny. Head black; antennae brown; 2nd segment lighter in middle; 3rd segment light brown



Fig. 103 *Rhyodes gracilis* n. sp. holotype ♂.

except at base; 4th segment often lighter apically. Pronotum with anterior margin, and a mid-longitudinal stripe in posterior half, pale; with a whitish spot in middle of posterior margin. Scutellum with a mid-longitudinal pale stripe in apical half (sometimes with a larger area pale). Corium with a longitudinal pale stripe on costal side extending to vein R+M and apically to the inward curving vein R. Femora brownish orange, with dark spots; tibiae orange, with a dark band at apex and base.

Structure. Size: ♂ – length 5.2–5.4, width 1.6; ♀ – length 5.55–6.10, width 1.7–2.0. Form slender, wings almost parallel sided, pronotum in both sexes only slightly wider at posterior than head; connexivum unexposed. Dorsum of head with semi-erect hairs near eyes only; lacking semi-erect hairs on hemelytra.

Head width to length 1.18 : 1.00 (1.23 : 1.06). Eye length 2× distance between anterior of eye and base of antenna, 0.4 : 0.2 (0.4 : 0.2). Width of vertex 2.25× eye width, 0.63 : 0.28 (3×, 0.74 : 0.25); vertex elevated above level of top of eyes; juga not

prominent. Antennal segments 0.35 : 0.80 : 0.70 : 0.75 (0.35 : 0.77 : 0.68 : 0.76); 1st segment with one-fifth of its length projecting beyond tip of tylus. Head in side view (Fig. 112) appearing short and thick. Rostrum reaching hind coxae; 1st segment almost, to just, reaching base of head.

Pronotum width to length 1.45 : 0.98 (1.68 : 1.04); sides straightish, not suddenly tapering anteriorly; punctuation on posterior lobe shallow, widely spaced. Scutellum width to length 0.80 : 0.65 (0.94 : 0.77); apex rounded, level. Membrane with 1A joining PCu (Fig. 10).

In ♀, abdominal sterna V and/or VI covered in middle; ovipositor cleft more than half as long as abdomen.

Genitalia. Paramere (Fig. 113) with blade of medium length, curved throughout, tapering. Aedeagus (Fig. 114) with small membranous lobe, apically inclined, near apex of conjunctiva; vesica (see also Fig. 115) with 3 main lobes; ejaculatory reservoir long.

Spermatheca (Fig. 116) with bulb intermediate between elongate and rounded; duct long, “disorganised”.

Type data. Holotype ♂ (5.4 × 1.6 mm), MK, Mt Sebastopol, 4800 ft (1464 m), on snowgrass (*Danthonia flavescens*), 8 Jan 1966, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (6 ♂ 7 ♀; BMNH, NZAC, USNM): 2 ♂ 2 ♀ same data as holotype; 3 ♀ same data, near top, on *Dracophyllum*; 2 ♂ same data as holotype except sweeping near top, J. I. Townsend; 1 ♂ OL, Coronet Peak, 3500 ft (1067 m), 16 Jan 1971, J. S. Dugdale and J. C. Watt; 1 ♂ same data, 1520 m, sweeping, 14 Feb 1976, L. L. Deitz; 1 ♀ MC, Porters Pass, on *Dracophyllum*, 17 Mar 1966, L. J. Dumbleton; 1 ♂ Christchurch, 16–18 Dec 1959, E. S. Gourlay.

Diagnosis. *R. gracilis* n. sp. is similar to *R. russatus* n. sp., but is distinguished from it by the greyish brown colour, and the wider longitudinal pale stripe, which extends beyond embolium to vein R+M and apically to the inward curving vein R.

Distribution. An alpine and lowland species taken from Mid Canterbury to Otago Lakes.

Biology. Adults and nymphs were taken on *Danthonia flavescens* and *Dracophyllum*. Some in the fifth instar were reared to adults.

Remarks. A slender species with genitalia intermediate between the type and *R. rupestris* n. sp. Fresh field specimens appear grey to the naked eye, but this may fade as collection specimens viewed under the microscope seem brown.

ryodes hirsutus n. sp.
fig. 6, 104, 117–119)



fig. 104 *Rhyodes hirsutus* n. sp. paratype ♀ (Kawekas).

characterised by the covering of very long, outstanding hairs, particularly on hemelytra and all tibiae, and distinctive colour banding on 2nd antennal segment.

Colour. Mostly brown; shiny. Head black; 1st and 2nd antennal segments black; 2nd segment orange, with a dark band at apex and base; 3rd segment orange, with a dark band at base. Pronotum brown, with darker punctures. Scutellum black, with a mid-longitudinal pale stripe in apical half to two-thirds, and often 2 pale spots on lateral arms of triradiate lge. Clavus and corium brown; apical angle of corium black or dark brown; corium sometimes with small, round, pale spots. Legs mostly pale orange; femora spotted, with a dark patch subapically; tibiae with a dark band at base.

Structure. Size: ♂ – length 5.70–5.96, width 1.9–2.4; ♀ – length 6.70–7.15, width 2.44–2.65. Form

oval; connexivum unexposed in ♂, usually unexposed in ♀ (narrowly exposed in some). Covered with very long, outstanding hairs, particularly on hemelytra and all tibiae (Fig. 6).

Head width to length 1.45 : 1.15 (1.47 : 1.20). Eye length 1.8× distance between anterior of eye and base of antenna, 0.45 : 0.25 (1.47×, 0.44 : 0.30). Width of vertex 2.45× eye width, 0.78 : 0.32 (2.94×, 0.88 : 0.30); vertex not elevated above eyes; juga prominent (Fig. 104). Antennal segments 0.47 : 1.03 : 0.80 : 0.95 (0.50 : 1.02 : 0.81 : 1.01); 1st segment with two-fifths of its length projecting beyond tip of tylus. Head in side view appearing short and thick. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 2.2 : 1.3 (2.27 : 1.42); sides straightish, not suddenly tapering anteriorly; punctuation on posterior lobe coarse, dense. Scutellum width to length 1.0 : 0.8 (1.35 : 1.00); apex acute, upturned.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 117) with blade short, curved throughout, tapering. Aedeagus (Fig. 118) with 3 main lobes on vesica; secondary gonopore with a wide, flat flare; ejaculatory reservoir with broad, triangular wings.

Spermatheca (Fig. 119) with bulb elongate, lying over.

Type data. Holotype ♀ (6.8×2.7 mm), HB, Kaweka Range, Makahu Spur, 4000 ft (1220 m), on *Senecio bidwillii*, 24 Feb 1971, A. C. Eyles (NZAC). Allotype ♂ same data as holotype, except taken as 5th instar nymph in *Celmisia spectabilis* subsp. *spectabilis* seedhead and reared to adult (NZAC). Paratypes (15 ♂ 19 ♀; AMNZ, BMNH, FRNZ, NMNZ, NZAC, USNM): 1 ♀ same data as holotype; 4 ♀ same data as holotype, except taken as 5th instar nymphs and reared to adults; 1 ♂ 1 ♀ same data as allotype (♂ at 1464 m); 3 ♂ 1 ♀ TO, Mt Ruapehu, 3800 ft (1160 m), 22 Feb 1965, J. S. Dugdale, FRI 37; 1 ♂ Whakapapa Valley, 4100 ft (1250 m), on bushline, 21 Nov 1962, J.S.D., FRI 40; 1 ♀ Mt Ruapehu, Whakapapa Stream, 3700 ft (1130 m), beaten from flowering *Hebe salicifolia*, 1 Mar 1959, J. C. Watt, Taumarunui Co; 1 specimen (abdomen missing), same data except on flowering *Olearia nummularifolia*; 1 ♀ National Park, Salt Hut track, 4500 ft (1372 m), subalpine scrub, 19 Oct 1949, E. G. Turbott, Taumarunui Co; 1 ♂ 1 ♀ TK, Mt Egmont, 4800 ft (1464 m), on *Hebe odera*, Nov 1963, J.S.D., FRI 32; 1 ♀ Mt Egmont, 1372–1524 m, 21 Nov

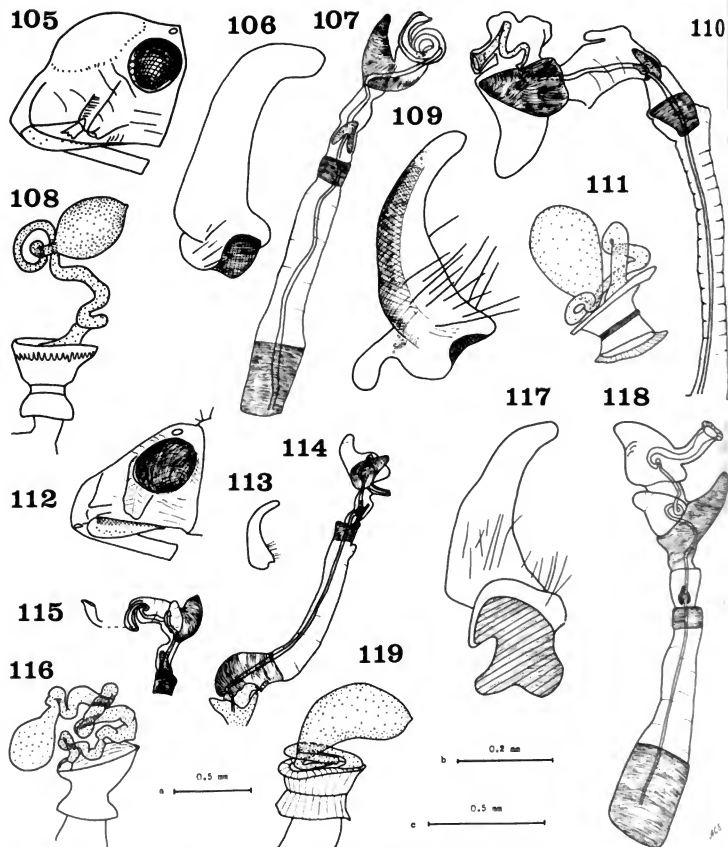


Fig. 105–119 105–108 *R. emimens* n. sp.: 105, head, side view of holotype ♂; 106, left paramere; 107, aedeagus (both of paratype ♂); 108, spermatheca of paratype ♀; 109–111 *R. depilis* n. sp.: 109, left paramere; 110, aedeagus (both of paratype ♂ killed, dissected in cop, Takahe Vly); 111, spermatheca of paratype ♀; 112–116 *R. gracilis* n. sp.: 112, head, side view; 113, left paramere viewed from above genital capsule (excludes articulating part); 114, aedeagus; 115, vesica, another aspect (all of paratype ♂ Mt Sebastopol); 116, spermatheca of paratype ♀ (Mt Sebastopol); 117–119 *R. hirsutus* n. sp.: 117, left paramere; 118, aedeagus (both of allotype ♂ Kawekas); 119, spermatheca of paratype ♀ (Kawekas) Fig. 105, 112–115 to scale a; 106, 108, 109, 111, 116, 117, 119 to scale b; 107, 110, 118 to scale c.

63, J.S.D., FRI 33; 1 ♂ 1 ♀ North Egmont, 915–120 m, 20 Nov 1963, J.S.D., FRI 34; 1 ♂ North Egmont, Holly Hut, 950 m, under *Uncinia rubra*, 28 Nov 1975, J.S.D.; 2 ♂ 2 ♀ Stratford, 4300 ft (1310 m), 20 Nov 1963, J.S.D., FRI 48; 1 ♂ 1 ♀ same data at FRI 50; 2 ♂ 1 ♀ SE Pouakai Range, Hukawakawa Swamp, 914 m, 27 Nov 1975, K. J. Cox; 2 ♂ 1 ♀ same data except sweeping tussock and a mat plants, J.S.D.; 1 ♀ BP, Rotoehu State Forest, Feb 1955, R. Zondag, FRI 12.

Other material examined. 1 ♂ in poor condition taken above Mangatepopo Hut, National Park, 26 Feb 1949, R. Harrison (NZAC).

Diagnosis. *R. hirsutus* n. sp. is distinguished from *R. badix* n. sp. by the very long, outstanding hairs on the hind tibiae and wings, and from *R. brevifissas* n. sp. by the distinctive colour banding on the second antennal segment, dense pronotal punctation, and longer ovipositor cleft.

Distribution. Taken on mountains across the centre of the North Island (Hawke's Bay, Taupo, Taranaki), but at a lower level in Bay of Plenty.

Biology. Breeds on *Senecio bidwillii* and *Celmisia spectabilis* subsp. *spectabilis*, as both adults and nymphs were taken on these plants. Nymphs (one per *Senecio* seedhead, several per *Celmisia* seedhead) were out of sight and protected under the parachute canopy. Adults have also been taken on *Hebe* (two specimens), *Olearia*, under *Uncinia rubra*, and on either tussock or mat plants.

Remarks. Genitalia and sides of pronotum typical.

Rhyodes jugatus n. sp.

(Fig. 2, 120, 125–127)

Characterised by the broad body (Fig. 120), convex vertex, pale straw colour, longish semi-erect hairs on hemelytra, widely spaced pronotal punctures, and short hairs on all tibiae.

Colour. Mostly pale, with some black; shiny. Head black; 1st antennal segment black, with pale base; 2nd and 3rd segments black or dark brown, with a narrow pale band at apex; 4th segment dark throughout. Pronotum mostly pale buff, with brown punctation; variable area around calli, brown. Scutellum black or brown, with a mid-longitudinal pale stripe in anterior half; obscure orange on side arms of triradiate ridge. Clavus and corium of uniform pale straw colour. Femora spotted, mainly underneath; tibiae pale except apically and basally.



Fig. 120 *Rhyodes jugatus* n. sp. allotype ♀.

Structure. Size: ♂ – length 5.5–5.8, width 2.1–2.2; ♀ – length 6.0–7.0, width 2.45–2.70. Form oval; macropterous and sub-brachypterous; connexivum usually at least partly exposed in ♀, unexposed in ♂. Hemelytra with longish erect or semi-erect hairs well distributed.

Head width to length 1.37 : 1.14 (1.45 : 1.20). Eye length 1.9× distance between anterior of eye and base of antenna, 0.42 : 0.22 (1.6×, 0.43 : 0.27). Width of vertex 2.4× eye width, 0.72 : 0.30 (2.6×, 0.81 : 0.31); vertex convex above level of top of eyes; juga prominent. Antennal segments 0.4 : 0.87 : 0.7 : 0.9 (0.46 : 0.95 : 0.80 : 0.99); 1st segment with one-fourth (♀ two-sevenths) of its length projecting beyond tip of tylus. Head in side view appearing short and thick (Fig. 2). Rostrum reaching hind coxae; 1st segment not reaching base of head.

Pronotum width to length 1.85 : 1.19 (2.18 : 1.34); sides straightish to slightly sinuate, not suddenly tapering anteriorly; punctation on posterior lobe coarse, widely spaced. Scutellum width to length 1.10 : 0.82 (1.32 : 1.01); apex acute, upturned.

In ♀, abdominal sterna V and VI uncovered in middle; ovipositor cleft less than half as long as abdomen (Fig. 2).

Genitalia. Paramere (Fig. 125) with blade short, curved throughout, tapering. Aedeagus (Fig. 126) with small membranous lobe near apex of conjunctiva; vesica with membranous lobe before sclerotised lobe; ejaculatory reservoir small, with neck non-bulbous, and wings curled outwards at base.

Spermatheca (Fig. 127) with bulb elongate, lying over.

Type data. Holotype ♂ (5.55 × 2.15 mm), MK, Mt Cook National Park, Sealy Lake track, on *Celmisia semicordata* subsp. *semicordata*, 10 Jan 1966, A. C. Eyles (NZAC). Allotype ♀ same data as holotype except taken at Sealy Lake (NZAC). Paratypes (8 ♂ 15 ♀; AMNZ, BMNH, NZAC, USNM): 1 ♂ same data as holotype; 2 ♀ same data as allotype; 1 ♀ Koa Point track, Sealy Lake, bush sweep, 10 Jan 1966, A.C.E.; 1 ♀ Mt Cook National Park, Blue Stream, 740 m, on *Ranunculus lyalli* flowers, 13 Nov 1976, W. J. Sweney; 1 ♀ Hooker Hut, 1100 m, on edelweiss (*Leucogenes grandiceps*) flower, 4 Feb 1977, W.J.S.; 1 ♀ OL, Bold Peak, 9 Jan 1920, C. E. Clarke Collection, Lake Co; 1 ♀ WD, upper Otira Valley, 3200 ft (975 m), on *Celmisia spectabilis* subsp. *spectabilis*, 14 Nov 1966, A. K. Walker; 1 ♂ 2 ♀ NC, Arthur's Pass, 3000 ft (915 m), 16–19 Dec 1959, J. I. Townsend and J. S. Dugdale; 1 ♂ Arthur's Pass, 8–11 Jan 1957, E. S. Gourlay; 1 ♀ Arthur's Pass, 2–3 Jan 1943, E.S.G.; 2 ♂ Arthur's Pass, 31 Jan 1958, J. Dumbleton (ex Dumbleton Collection); 1 ♂ 1 ♀ Cass, 10 Nov 1924, A. Tonnoir; 1 ♀ MB, Black Birch Station, on *Cassinia*, 17 Feb 1970, A.C.E.; 1 ♀ Red Hills Plateau, 3700 ft (1130 m), 22 Mar 1972, J.S.D.; 1 ♀ NN, Mt Domett, 1250 m, 1 Dec 1971, G. Kuschel; 1 ♂ same data except 1350 m; 1 ♂ same data except 1000–1450 m, J.S.D.; 1 ♀ Karama River, Moonstone Lake, ex moss, 8 Feb 1973, A.K.W.

Other material examined. 1 specimen (in poor condition with abdomen missing) Mt Arthur, 4500 ft (1372 m), 26 Feb 1921, A. Philpott (NZAC).

Diagnosis. *R. jugatus* n. sp. is similar to the robust *R. stewartensis* in the widely spaced pronotal punctures and prominent juga, but is distinguished from it by the erect hairs on hemelytra, longer rostrum, shorter first rostral segment, convex vertex, and upturned apex of scutellum.

Distribution. Taken on mountain ranges in the South Island from Marlborough and Nelson to Te Anau.

Biology. Taken on and no doubt lives on *Celmisia* species. Also taken on *Ranunculus lyalli* and *Leucogenes grandiceps*.

Remarks. Genitalia and sides of pronotum typical.

Rhyodes koebelei n. sp.
(Fig. 121, 122, 128–131)



Fig. 121 *Rhyodes koebelei* n. sp. paratype ♀ col. Koebele.

Characterised by the pale orange head with distinctive black markings, very short, rather thick, orange 1st antennal segment with 2 dark bands, pale orange 2nd and 3rd antennal segments with narrow dark band at base, shallow dense punctation on posterior pronotal lobe, and the very long, outstanding hairs on fore tibiae.

Colour. Brown to light orange brown; shiny. Head mostly pale orange, with distinctive black markings in posterior half (Fig. 128); 1st antennal segment pale orange, with a narrow dark band at apex and a dark dotted band about middle (Fig. 128); 2nd and



122 Distribution of *Rhyodes koebelei* n. sp.

segments paler orange, with a narrow dark band base; 4th segment orange. Scutellum sometimes black brown to black in basal depression, basal angles on sides to apex. Clavus sometimes dark in basal f near scutellum and on claval commissure. rium may have some darker areas each side of n Cu. Femora lightly spotted, with a pale spot at x; tibiae pale. Ventral surface of abdomen and rax mainly light orange.

Structure. Size: ♂ – length 5.0–5.7, width 1.7–2.1; ♀ – length 5.8–6.8, width 2.05–2.55. Form oval g. 121; body flattened; connexivum at least tly, sometimes broadly, exposed in ♀, unexposed ♂. Hemelytra with semi-erect hairs well tributed; fore tibiae with long, outstanding hairs; d tiabiae with long and short hairs.

Head width to length 1.26 : 0.98 (1.37 : 1.08). e length 1.95× distance between anterior of eye d base of antenna, 0.37 : 0.19 (1.8×, 0.41 : 0.23). idth of vertex 2.8× eye width, 0.73 : 0.26 (3.25×, 34 : 0.26); vertex not elevated above eyes; juga ominent. Antennal segments 0.35 : 0.80 : 0.62 : 57 (0.39 : 0.84 : 0.67 : 0.75); 1st segment with

about one-fourth of its length projecting beyond tip of tylus. Head in side view short and thick. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.7 : 1.0 (2.0 : 1.18); sides straightish, to gently sinuate, not suddenly tapering anteriorly; punctation on posterior lobe shallow, dense. Scutellum width to length 0.97 : 0.81 (1.11 : 0.84); apex acute, upturned.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft less than half as long as abdomen.

Genitalia. Paramere (Fig. 129) with blade short, curved throughout, tapering. Aedeagus (Fig. 130) with a small, membranous lobe near apex of conjunctiva, and possibly another lobe in sclerotised part; ejaculatory reservoir with broad, triangular wings.

Spermatheca (Fig. 131) with bulb elongate, lying over.

Type data. Holotype ♀ (5.5 × 2.4 mm), NN, Maitai Valley, swept off *Kunzea ericoides*, 6 Nov 1951, L. Gurr (NZAC). Allotype ♂ CO, Tarras, 1000 ft (305 m), 16–22 Jan 1954, E. S. Gourlay (NZAC). Paratypes (32 ♂ 49 ♀; AMNZ, BMNH, CASC, CMNZ, FRNZ, NMNZ, NZAC, USNM): 1 ♀ same data as holotype; 1 ♂ Maitai Reserve, sweeping grass, 20 Jan 1971, G. Abercrombie; 1 ♀ Nelson, Dec 1951, A. W. Parrott; 1 ♂ Nelson, 16 Oct 1927, E. S. Gourlay; 2 ♂ Botanical Hill, Nelson, 17 Feb 1975, A. K. Walker; 1 ♂ same data except on *Macropiper excelsum*, 26 Sep 1967, J. C. Watt; 7 ♀ Aniseed Valley, 20 Mar 1951, A. Carson (No. 37/51); 3 ♂ 1 ♀ same data except A. W. P. (No. 39/51); 2 ♂ Aniseed Valley, sweeping long grass and trees, 1950, A. W. P. (No. 28/50); 1 ♀ Richmond, sweeping grass, 1950, A. W. P. (No. 31/50); 1 ♀ Tapawera, 4 Jan 1923, R. J. Tillyard; 1 ♂ 1 ♀ Golden Downs, 17 Oct 1957, R. F. L., FRI 26; 3 ♀ Tinline Valley, sweeping long grass in bush clearing, 17 Oct 1951, A. W. P.; 1 ♀ Cobb Valley, on *Rubus australis*, 4 Apr 1961, J. G. R. McBurney, FRI 13; 7 ♂ 2 ♀ CO, same data as allotype; 1 ♀ DN, Leith, 7 Nov 1916; 1 ♂ 1 ♀ Ross Creek Reservoir, 13 Apr 1980, B. I. P. Barratt; 1 ♀ KA, The Doone, Inland Kaikoura Range, on *Leptospermum scoparium*, 17 Mar 1976, R. P. Macfarlane; 1 ♀ Conway Flats, same host plant, 7 Nov 1970, R. P. M., labelled “*Rhyodes* sp. Det. L. Deitz 1959”; 1 ♂ 1 ♀ Conway Flats, on *Gladiolus* sp., 30 Dec 1974; 1 ♂ SD, French Pass, Feb 1971, G. W. Ramsay; 1 ♀ WN, Wellington, 22 Nov 1919, labelled “*Nysius clavicornis*”; 1 ♀ WA, Greytown, on lucerne, 8 Apr 1959, A. C. Eyles, labelled “Hc, 34

Rhyodes sp., Det. A. C. Eyles 1959"; 1 ♀ WI, Komako, Easter 1957; 1 ♀ TO, Waiotapu, on manuka, 12 Nov 1970, A.C.E.; 1 ♀ GB, Gisborne, 4 Nov 1955, R. Zondag, FRI 9; 1 ♀ BP, Whakarewarewa, 23 Aug 1950, G.B.R., FRI 1; 1 ♀ Tarawera, 11 Nov 1919, labelled "*Nysius clavicornis*"; 1 ♂ Mt Te Aroha, 975 m, beating *Nothofagus menziesii*, 21 Oct 1967, J. C. Watt; 1 ♂ 1 ♀ CL, Kauaeranga State Forest, taken in cop., 4 Oct 1963, P. S. Crowhurst, FRI 27; 1 ♂ 1 ♀ Mayor Island, Opo Bay, Nov 1959, J.C.W.; 1 ♂ Great Barrier Island, Motairche, 20 Nov 1964, R. G. Ordish; 1 ♂ same data except on manuka, 15 Nov 1964, F. M. O'Brien; 1 ♀ Little Barrier island, 4–12 Mar 1929, W. R. B. Oliver; 1 ♂ ND, Whangarei Harbour, on Pohutukawa flower, 26 Nov 1959, S. M. Cop, FRI 14; 1 ♀ Chickens Islands, Coppermine Island, beating scrub, 28–31 Oct 1968, J.C.W.; 1 ♀ Paihia Beach, ex *Polygala myrrifolia*, 15 Oct 1977, Archibald; 1 ♂ Kerikeri, Opito Bay, on manuka, 14 Feb 1965, J. G. Brown; 1 ♀ S of North Cape, beating low *Leptospermum*, light, 7 Oct 1948, E. G. Turbott, Mangonui Co; 1 ♂ Spirits Bay, Waitanoni Stream, 7 Nov 1967; 2 ♂ 10 ♀ no data labels (CMNZ); 1 ♀ Australia [in error], Koebele (Koebele Collection).

Diagnosis. *R. koebelei* n. sp. is distinguished from *R. clavicornis* by the absence of triangular plate-like projections on posterior margin of pronotum, and the colour of antennal segments, and from nearly all species of *Rhyodes* by the distinctive black head markings on an orange background, and the very short, rather thick first antennal segment.

Distribution. *R. koebelei* is widely distributed in New Zealand (Fig. 122) and from its abundance in collections must be regarded as common. It probably occurs in Canterbury as there are many specimens in the Canterbury Museum without data labels. It also occurs on Coppermine, Mayor, Little Barrier, and Great Barrier Islands. Unlike most of the species in the genus, this is a lowland species.

Biology. Taken on manuka, kanuka, pohutukawa, *Rubus australis*, *Macropiper excelsum*, *Nothofagus menziesii*, *Polygala myrrifolia*, *Gladiolus* sp., grass, and lucerne. As five different collectors have taken *R. koebelei* on manuka and the author has collected several specimens on flowering manuka at Waiotapu, this can be regarded as a definite host association as probably can the related kanuka. It has been taken on several occasions by sweeping grass.

Remarks. Named after the entomologist A. Koebele who collected the first specimen on a trip to Australia and New Zealand in 1888–89. *Rhyodes* is an endemic New Zealand genus which does not occur

in Australia. The Koebele specimen label "Australia" is indeed an error as mentioned by Usinger (1942b). Both countries have a Great Barrier. *R. koebelei* n. sp. has been confused with *R. clavicornis* and in collections has often been placed with specimens under that name. Usinger (1942b) mentioned the Koebele specimen under *clavicornis*, and the Taupo specimen he saw probably belongs in the new species too. The specimen Hc. 34 taken by Eyles (1967) which he listed as "*R. clavicornis*?" and labelled "*Rhyodes* sp." belongs in *R. koebelei*. Sides of pronotum and genitalia typical.

***Rhyodes longiceps* n. sp.**
(Fig. 123, 132–134, 138, 139)



Fig. 123 *Rhyodes longiceps* n. sp. holotype ♂.

Characterised by the narrow body, greyish color, sinuate sided pronotum (Fig. 123), and point of origin of antennal tubercle at anterior margin of pronotum. Colour. Mainly brown, with pubescence giving

reish appearance; shiny. Head black; antennae lack, 2nd and 3rd segments with a pale band at apex wider on 3rd; antenniferous tubercles black throughout. Pronotum with 3 pale spots just behind anterior margin; posterior lobe with 4 longitudinal rown stripes. Scutellum black, with a midngitudinal pale stripe in apical half. Clavus and orium faintly mottled with small, pale spots. Femora ark, with a pale spot at apex; mid and hind femora ♀ pale basally underneath, with dark spots; tibiae ale in middle.

Structure. Size: ♂ – length 5.2–5.5, width 1.80–.95; ♀ – length 5.6–6.2, width 2.0–2.3. Form oval; ody narrow; connexivum usually slightly or partly xposed in ♀ (and sometimes in ♂). Hemelytra with emi-erect hairs well distributed; fore tibiae with ong, outstanding hairs; mid tibiae with a few long, outstanding hairs and more short hairs (as in Fig. 5).

Head width to length 1.23 : 1.08 : (1.28 : 1.09). Eye length 2× distance between anterior of eye and ase of antenna, 0.4 : 0.2 (1.75×, 0.40 : 0.23). Width if vertex 2.25× eye width, 0.68 : 0.30 (2.5×, 0.73 : 1.29); vertex not elevated above eyes; juga prominent. Antennal segments 0.4 : 0.8 : 0.7 : 0.8 (0.4 : 0.8 : 0.65 : 0.8); 1st segment with one-third of its length projecting beyond tip of tylus. Head in side view with antennal tubercle arising level with anterior margin of eye (Fig. 132); portion of head between front of antennal tubercle and tip of tylus gradually tapering so that head appears long and narrow. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.68 : 1.10 (1.80 : 1.14); sides sinuate, not suddenly tapering anteriorly; punctuation on posterior lobe coarse, dense. Scutellum width to length 0.95 : 0.83 (1.00 : 0.85); apex acute, upturned.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 133) with blade short, curved throughout, tapering. Aedeagus (Fig. 134) with 3 main lobes on vesica; ejaculatory reservoir with broad, triangular wings.

Spermatheca (Fig. 139) with bulb elongate, lying over. Ring sclerites (Fig. 138) smaller than spermathecal bulb.

Typedata. Holotype ♂ (5.5×1.9 mm), OL, Coronet Peak, 12 Jan 1966, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (4 ♂ 9 ♀; BMNH, NZAC, USNM): 3 ♂ 6 ♀ same data as holotype, on *Celmisia*; 1 ♀ same locality, summit,

4500–5000 ft (1372–1524 m), 2 Dec 1963, J. I. Townsend; 1 ♀ same data, on flowers and under stones, 12 Jan 1966, J.I.T.; 1 ♂ 1 ♀ Coronet Peak, 3820 ft (1165 m), 8 Dec 1966, A. K. Walker.

Other material examined. 38 specimens (AMNZ, FRNZ, NZAC, Otago Museum): 1 ♂ OL, end Hollyford Road, general beating, 9 Dec 1966, K. Z. Wilson; 3 ♂ 4 ♀ Hollyford Valley, Key summit, 2600 ft (793 m), *Cassinia* and *Dracophyllum*, 12 Jan 1967, A. K. Walker; 1 ♂ Routeburn, Harris Saddle, 25 Jan 1926, C. E. Clarke Collection, Lake Co, South Island; 1 ♂ SL, Takitimu Mts, 1000–3000 ft, on *Celmisia semicordata* subsp. *stricta*, 3 Nov 1962, A. C. Eyles; 1 ♀ FD, Mt Luxmore, 3500 ft (1067 m), 22 Feb 1965, J. S. Dugdale, FRI 36; 1 ♀ Wilmot Pass, Mt Barber, 1047 m, on *Celmisia petrii*, Manapouri Exp., Jan 1970, A.C.E.; 4 ♂ 1 ♀ above Homer Tunnel, 4300 ft (1310 m), general beating, 13 Jan 1967, A.K.W.; 1 ♂ 1 ♀ W Olivine Range, Simonin Pass, 1036 m, sweeping, 23 Jan 1975, J.S.D.; 1 ♂ W Olivine Range, Tempest Spur, sweeping, 29 Jan 1975, J.S.D.; 7 ♂ 3 ♀ Darran Mts, Tutoko Bench, 945–1524 m, some by sweeping grassland, 8–14 Jan 1977, T. K. Crosby and J.S.D.; 1 ♀ CO, Dunstan Range, 1524–1626 m, 13 Jan 1971, P. Child; 1 ♀ MK, Mt Sebastopol near top, on flower of small *Celmisia*, 8 Jan 1966, A.C.E.; 1 ♂ Mt Cook National Park, 1200 m, on *Celmisia* flower, 7 Jan 1977, W. J. Sweeney; 1 ♂ same data except 740 m, on pool, 14 Nov 1976; 1 ♀ Sealey Range, 1500 m, under stone under *Celmisia* and *Aciphylla divisa*, 16 Jan 1977, W.J.S.; 1 ♂ Sefton Biv., 1710 m, 29 Nov 1976, W.J.S.; 1 ♂ 1 ♀ MC, Mt Wakefield, 2200–3500 ft, FRI 47.

Diagnosis. *R. longiceps* n. sp. is distinguished from *R. spadix* n. sp. by the greyish colour, narrower body, sinuate sided pronotum, antennal tubercle arising level with anterior margin of eye, and the portion of head between front of antennal tubercle and tip of tylus gradually tapering so that head appears longer and narrower.

Distribution. A high altitude species occurring on mountain ranges in the southern half of the South Island.

Biology. Host plants *Celmisia semicordata* subsp. *stricta* and *Celmisia petrii*. Also taken on *Cassinia* and/or *Dracophyllum* and sweeping grass. This species and *R. celmsiae* n. sp. were found at higher levels and the summit of Coronet Peak, whereas *R. myersi* was found on the lower slopes.

Remarks. Typical for genitalia and more or less for sides of pronotum. The type series has been limited to material from Coronet Peak.

Rhyodes longirostris n. sp.
(Fig. 124, 135–137)



Fig. 124 *Rhyodes longirostris* n. sp. paratype ♂.

Characterised by the hairiness, 4 dark stripes on pronotum, and very long rostrum.

Colour. Pale straw coloured (Fig. 124), with some black; shiny. Head black; 1st and 4th antennal segments black; 2nd and 3rd segments black, with a narrow pale band at apex (that on III 2× as wide as on II). Pronotum with 4 longitudinal black stripes, 1 each side of midline and 2 sublaterally. Scutellum black, with a mid-longitudinal pale stripe in apical two-thirds, and a pale spot near each basal angle. Claval commissure and apical angle of corium dark. Femora with a pale spot at apex; remainder of fore femora black; mid and hind femora black or brown apically, but yellow basally, spotted with brown underneath; tibiae pale, with brown band at apex and base.

Structure. Size: ♂ – length 6.40–6.85, width 2.3–2.5; ♀ – length 6.5–7.3, width 2.50–2.85. Form elongate oval; connexivum partly exposed in both sexes (broadly exposed in some ♂). Spiracle VII in

outer sixth of connexivum. Semi-erect hairs well distributed on hemelytra. Fore and mid tibiae with long, outstanding hairs; hind tibiae with a few long hairs, most equal to width of tibia in middle, some shorter.

Head width to length 1.36 : 1.20 (1.45 : 1.24). Eye length 1.55× distance between anterior of eye and base of antenna, 0.41 : 0.26 (1.46×, 0.41 : 0.28). Width of vertex 2.85× eye width, 0.80 : 0.28 (3.1×, 0.88 : 0.28); vertex convex above level of top of eyes; juga prominent. Antennal segments 0.47 : 1.02 : 0.71 : 0.82 (0.48 : 1.05 : 0.74 : 0.90); 1st segment with one-third to one-fourth of its length projecting beyond tip of tylus. Head in side view long and narrow. Rostrum reaching beyond hind coxae; 1st segment reaching base of head.

Pronotum width to length 2.09 : 1.34 (2.27 : 1.35); sides slightly sinuate, not suddenly tapering anteriorly; punctuation on posterior lobe coarse, widely spaced. Scutellum width to length 1.16 : 0.94 (1.26 : 0.99); apex rounded, upturned.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft more than half as long as abdomen.

Genitalia. Paramere (Fig. 135) with blade short, curved throughout, tapering. Aedeagus as in Fig. 136; ejaculatory reservoir with wings more or less triangular.

Spermatheca (Fig. 137) with bulb elongate (constricted near base at least in this specimen), lying over; flange with upper lip rolled.

Type data. Holotype ♂ (6.4 × 2.4 mm), GB, Mt Arawhano, 3900 ft (1190 m), on *Celmisia spectabilis* subsp. *spectabilis*, 1 Mar 1971, A. C. Eyles (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (10 ♂ 8 ♀; BMNH, NZAC, USNM): 4 ♂ 4 ♀ same data as holotype (except 2 at 1100 m, 2 at 1160 m); 2 ♂ 2 ♀ same data as holotype except 1130 m, A.C.E. and J. I. Townsend; 1 ♂ same data except 1100 m, J.I.T.; 1 ♂ 2 ♀ same data except 3000 ft (915 m), J.I.T., collected as 5th instar nymphs and reared to adults; 2 ♂ Mt Arawhano, 3800–4000 ft, 1 Mar 1971, A.C.E.

Other material examined. 1 ♀ (taken with type series) with part of nymphal exuvium still present on wings, top of prothorax, and top of head. If part of exuvium is lifted, adult wings are seen to be there, but unexpanded; eyes small.

Diagnosis. *R. longirostris* n. sp. very closely resembles the South Island *R. myersi*, but is easily distinguished from it by the long, outstanding hairs on fore and mid tibiae and antennae, semi-erect hairs

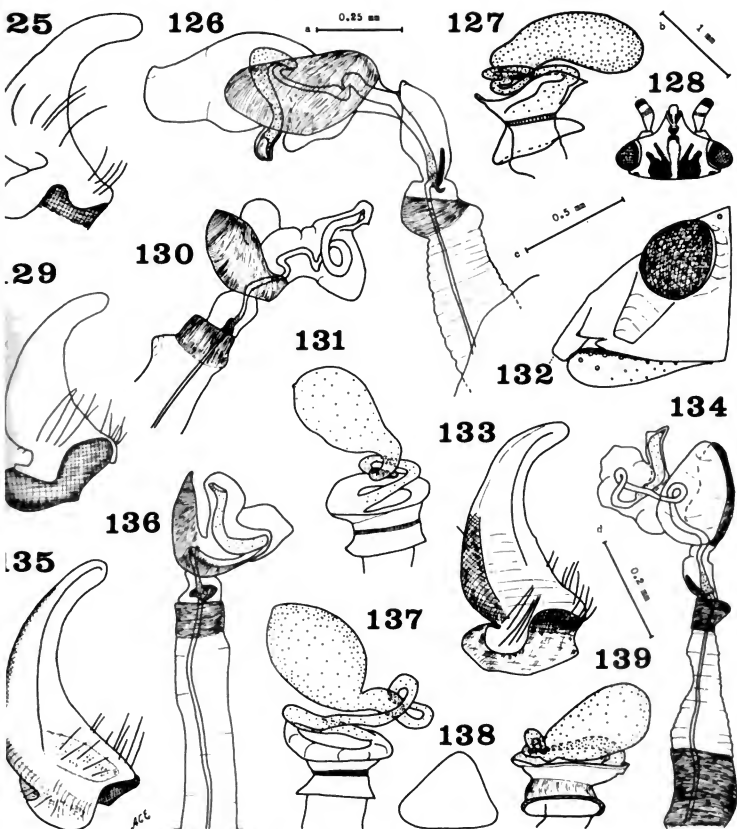


Fig. 125-139 125-127 *R. jugatus* n. sp.: 125, left paramere; 126, aedeagus (both of paratype ♂ killed, dissected in op); 127, spermatheca of paratype ♀ (both Sealy Lake); 128-131 *R. koebelei* n. sp.: 128, head, dorsal view of paratype ♂ (Greytown); 129, left paramere; 130, aedeagus (both of paratype ♂ Tarras); 131, spermatheca of paratype ♀ (Anisede fly); 132-134 *R. longiceps* n. sp. paratype ♂: 132, head, side view; 133, left paramere; 134, aedeagus; 135-137 *R. angiostris* n. sp.: 135, left paramere; 136, aedeagus (both of paratype ♂); 137, spermatheca of paratype ♀; 138-139 *R. longiceps* n. sp. paratype ♀: 138, ring sclerite; 139, spermatheca. Fig. 126 to scale a; 128 to scale b; 132 to scale c; 25, 127, 129, 131, 133, 135, 137-139 to scale d; 130, 134, 136 to half scale d.

on hemelytra, and longer rostrum reaching beyond hind coxae.

Distribution. So far known only from 900–1200 m on Mt Arawhano, Gisborne area.

Biology. Breeds on *Celmisia spectabilis* subsp. *spectabilis* as both adults and nymphs were taken on this plant. Nymphs were on top of and in the seedheads, several per seedhead, out of sight and protected under the parachute canopy. They were feeding on the seeds.

Remarks. Pronotum and genitalia typical. *R. myersi* does not occur in the North Island. It would be interesting to know if it ever did. For a similar situation see remarks under *R. brevifissas* n. sp. and *R. stewartensis*.

***Rhyphodes myersi* Usinger**
(Fig. 140, 141, 146–151)



Fig. 140 *Rhyphodes myersi* Usinger ♂ (Black Birch Ra.).



Fig. 141 Distribution of *Rhyphodes myersi* Usinger.

Rhyphodes myersi Usinger 1942b: 47–49 (Original description; keyed).

Rhyphodes myersi: Slater 1964: 345 (Catalogue).

Rhyphodes myersi: Ashlock 1967: 56 (List).

Rhyphodes myersi: Eyles 1974: 955–956 (Host plant; characters; Fig.).

Rhyphodes myersi: Wise 1977: 122 (List).

Rhyphodes myersi: Ueshima & Ashlock 1980: 733–734, 793 (Chromosomes).

Characterised by the pale banding on antennae, short, thick 1st antennal segment, convex vertex, lack of semi-erect hairs on hemelytra, with the more parallel sided body and large size.

Colour. Mainly pale buff or straw coloured (Fig. 140); shiny. Head black (sometimes with a narrow pale stripe on edges of vertex); antennae black, 2nd and 3rd segments with a bright, pale band at apex. Pronotum with 4 longitudinal dark stripes, 1 each side of midline and 2 sublaterally. Scutellum black, with a mid-longitudinal pale stripe in apical half, and 2 obscure pale stripes laterally in basal half. Clavus and corium almost uniformly pale buff or straw coloured, (sometimes with a brown stripe following vein Cu); claval commissure, and sometimes apical angle of corium, brown. Femora with a bright yellow spot near apex; remainder of fore femora dark; mid

d hind femora spotted underneath at least in basal 1/2, but dark on dorsal and posterior aspects; tibiae 1/2, with dark base and apex.

Structure. Size: ♂ – length 6.5–7.2, width 2.15–2.50; ♀ – length 7.2–8.1, width 2.35–2.75. Form elongate oval; connexivum unexposed to partly exposed in both sexes (broadly exposed in some ♀). Erect semi-erect hairs on hemelytra.

Head width to length 1.31 : 1.19 (1.35 : 1.24). Eye length 1.55× distance between anterior of eye and base of antenna, 0.41 : 0.26 (1.4×, 0.38 : 0.27). Width of vertex 2.85× eye width, 0.77 : 0.27 (3×, 0.81 : 0.27); vertex convex above level of top of eyes; gena prominent. Antennal segments 0.45 : 0.99 : 0.74 : 0.90 (0.47 : 1.04 : 0.78 : 0.93); 1st segment short and thick, with two-ninths (♀ almost one-fourth) of its length projecting beyond tip of tylus. Head in side view appearing long and narrow (Fig. 146). Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 2.09 : 1.34 (2.31 : 1.39); sides straightish to slightly sinuate, not suddenly tapering anteriorly; punctation on posterior lobe coarse, widely spaced. Scutellum width to length 1.15 : 0.94 (1.29 : 1.00); apex rounded, flattened (sometimes only slightly in both characters).

In ♀, abdominal sternum VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 147) with blade short, curved throughout, tapering. Aedeagus as in Fig. 148; ejaculatory reservoir (Fig. 149) with large, triangular wings curled at edges.

Spermatheca (Fig. 150) elongate, lying over. Egg sclerites (Fig. 151) smaller than spermathecal alba.

Material examined. Holotype ♀ (7.5 × 2.6 mm), C. Arthur's Pass, 3500 ft (1067 m), 22 Dec 1922, G. Myers (USNM). Paratype ♀ same data as holotype, 2800 ft (CASC). Plus 186 specimens (RNZ, NMNZ, NZAC).

Diagnosis. *R. myersi* is distinguished from *R. longirostris* n. sp. by the absence of semi-erect hairs on hemelytra, and the absence of longish, outstanding hairs on all tibiae.

Distribution. Occurs on mountains (1000–6000 ft or 300–1830 m) throughout the South Island (Fig. 41).

Ecology. Breeds on more than one species of *Celmisia* as it has been taken in numbers on these plants (especially *Celmisia spectabilis* or *Celmisia micordata*) on many mountains from Mt Arthur to

the Takitimu Mountains. Nymphs (several per seedhead) feed on the seeds out of sight protected by the parachute canopy. Several nymphs, provided with *Celmisia* seeds, were reared through to adults. Further information including species and subspecies of hosts is given in Tables 3 and 4. Some adults were taken on speargrass (*Aciphylla*) and large numbers of adults were found sheltering in the layers of dead leaves under these plants. Several adults were also taken on two species of *Cassinia*.

In one day's collecting on Coronet Peak, two species, *R. celmisiae* n. sp. and *R. longiceps* n. sp., were taken on *Celmisia* plants at medium and high altitudes including the summit, but *R. myersi* was found only on the lower slopes. As *myersi* occurs up to high altitudes on other mountains where these two new species do not occur, the finding suggests a zoning, through competition, on Coronet Peak.

Remarks. Genitalia and sides of pronotum typical.

Rhyodes rupestris n. sp.

(Fig. 9, 12, 20, 32, 142, 152–156)

Characterised by the shape of pronotum and parameres, flattened body, very short pubescence, and absence of erect or semi-erect hairs except on anterior lobe of pronotum.

Colour. Dull charcoal grey. Antennae dark grey. Pronotum with 2 large, pale areas on posterior lobe laterally and a small one in middle of posterior margin. Scutellum pale on lateral arms of triradiate ridge. Corium with small, round, pale spots. Legs dark; hind femora distinctly spotted underneath in basal half.

Structure. Size: ♂ – length 4.55–5.20, width 1.7–2.0; ♀ – length 5.25–6.35, width 2.1–2.4. Form egg-shaped; body flattened; connexivum at least partly exposed, often broadly exposed in both sexes. Lacking long, erect, or semi-erect hairs except on anterior lobe of pronotum; pubescence very short.

Head width to length 1.14 : 1.08 (1.28 : 1.12). Eye length 1.2× distance between anterior of eye and base of antenna, 0.34 : 0.29 (1.1×, 0.37 : 0.34). Width of vertex 2.75× eye width, 0.66 : 0.24 (3.1×, 0.77 : 0.25); vertex convex above level of top of eyes; gena not prominent. Antennal segments 0.48 : 0.85 : 0.60 : 0.64 (0.50 : 0.84 : 0.64 : 0.67); 1st segment with three-eighths (♀ two-fifths) of its length projecting beyond tip of tylus. Head in side view (Fig. 152) appearing long and narrow. Rostrum reaching beyond hind coxae; 1st segment reaching base of head.



Fig. 142 *Rhypodes rupestris* n. sp. holotype ♂.

Pronotum width to length 1.56 : 1.02 (1.84 : 1.13); sides sinuate, flaring to well developed, elevated posterolateral corners (Fig. 142, 153); punctation on posterior lobe shallow, dense. Scutellum width to length 0.84 : 0.68 (1.01 : 0.77); triradiate ridge prominent; apex rounded, prominently upturned.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft more than half as long as abdomen (Fig. 32).

Genitalia. Paramere (Fig. 154) with blade long, broad, almost straight for part of its length, not tapering. Aedeagus (Fig. 155) with a membranous lobe near apex of conjunctiva; vesica with 2 membranous lobes before sclerotised lobe; secondary gonopore widely flared; ejaculatory reservoir with narrow wings.

Spermatheca (Fig. 156) with bulb rounded or lemon-shaped; flange with upper lip noticeably rolled.

Type data. Holotype ♂ (5.15 × 1.95 mm), MB, Black Birch Station, 1463 m, under *Helichrysum coralloides*, 18 Feb 1970, A. C. Eyles (NZAC); taken as fifth-instar nymph which moulted to adult. Allotype ♀ same data as holotype (NZAC). Paratypes (10 ♂ 8 ♀; BMNH, NZAC, USNM): 7 ♂ 5 ♀ same data as holotype (1 ♀ taken as adult); 3 ♂ 2 ♀ Black Birch Station, 1402 m, under *H. coralloides* on rocks in front of house, 19 Feb 1970, A.C.E.; 1 ♀, Altmarlock Peak, 1463–1524 m, 17 Feb 1970, J.S. Dugdale.

Diagnosis. *R. rupestris* n. sp. is distinguished from *R. eminens* n. sp. by the lack of an elevated mound on the head, and from *R. brevipilis* n. sp. by the longer rostrum and the long, wide blade of the paramere.

Distribution. A high altitude species so far known only from Black Birch Station, Marlborough.

Biology. Found in February in a very exposed situation on a scree at the head of a chute at 1463 m. Wind was screaming up the chute, whistling amongst the rocks, and this species was breeding there, crouching against the rock under tiny shrublets of *H. coralloides*, sparsely spaced, and the only vegetation around on the larger rocks for several metres. Both adults and nymphs were taken; fifth-instar nymphs are similar in colour to adults. The flattened body may facilitate sheltering in crevices in rocks.

Remarks. This species and *R. eminens* n. sp., although different from all other species of *Rhypodes* in the very short pubescence and elevation of the pronotum, cannot be separated from the genus because they share one character (markedly sinuate sided pronotum) with *R. brevipilis* n. sp. and *R. bucculentus* n. sp., and another character (paramere and spermatheca shape) with *R. sericatus* and *R. argenteus* n. sp.

Rhypodes russatus n. sp.
(Fig. 143, 157–161)

Characterised by the slender body (Fig. 143), red colour, narrow, longitudinal, pale wing stripe, and shape of parameres and spermatheca.

Colour. Mostly red; shiny. Head black; 1st antennal segment black; 2nd segment black, with an orange band (not always evident) just beyond middle; 3rd segment orange, with a dark band at base; 4th segment dark brown, lighter in apical half. Scutellum black basally, sometimes laterally. Corium with pale embolium. Femora orange, with brown spots; tibiae pale orange, with apex dark.



Fig. 143 *Rhyodes russatus* n. sp. paratype ♀ (Mt Arthur).

Structure. Size: ♂ – length 5.2–5.5, width 1.65–1.75; ♀ – length 5.75–6.70, width 1.90–2.35. Form slender, wings almost parallel sided, pronotum in both sexes only slightly wider at posterior than head; annexivum partly exposed in ♀, unexposed in ♂. Pubescence sparse; hemelytra with semi-erect hairs usually only evident near base of clavus and corium.

Head width to length 1.22 : 0.99 (1.29 : 1.03). Head length 2.7× distance between anterior of eye to base of antenna, 0.40 : 0.15 (2×, 0.4 : 0.2). Width of vertex 2.25× eye width, 0.65 : 0.29 (2.55×, 0.74 : 0.29); vertex not elevated above eyes; jugal not prominent. Antennal segments 0.38 : 0.80 : 0.66 : 0.79 (0.38 : 0.73 : 0.63 : 0.73); 1st segment with two-thirds (♀ one-third) of its length projecting beyond base of tylus. Head in side view (Fig. 157) appearing short and thick. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.53 : 1.03 (1.76 : 1.13); sides straightish, not suddenly tapering

anteriorly; punctuation on posterior lobe coarse, widely spaced. Scutellum width to length 0.84 : 0.70 (1.03 : 0.81); apex rounded, level. Membrane with 1A joining PCu (as in Fig. 8).

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft more than half as long as abdomen.

Genitalia. Paramere (Fig. 158) with blade of medium length, curved throughout, tapering. Aedeagus (Fig. 159) with small membranous lobe near apex of conjunctiva; vesica with small lobe before 2 ear-like lobes, and 1 other lobe distally; ejaculatory reservoir (Fig. 160) with wide, flat wings.

Spermatheca (Fig. 161) with bulb intermediate between elongate and rounded; duct long, “disorganised”.

Type data. Holotype ♂ (5.50 × 1.75 mm), NN, Mt Arthur, 1250 m, on *Dracophyllum*, 22 Mar 1971, G. Kuschel (NZAC). Allotype ♀ same data as holotype except A. C. Eyles (NZAC). Paratypes (10 ♂ 8 ♀; BMNH, TFP, NZAC, USNM): 2 ♂ 1 ♀ same data as holotype; 2 ♀ Mt Arthur, 3000–4000 ft (915–1250 m), 3 Feb 1965, G. K. and A. K. Walker; 1 ♂ 1 ♀ same data as allotype (♀ on *Cassinia vauvilliersii*); 1 ♂ 1 ♀ NC, Phipps’s Peak, 5500 ft (1677 m), 29 Oct 1955, B. B. Given; 1 ♂ 1 ♀ MB, Island Saddle, NE of Lake Tennyson, 1372 m, sweeping tussock, 21 Jan 1976, A. K. Walker; 1 ♀ KA, Mt Percival, on *Helichrysum selago*, 29 Oct 1962, A. C. Eyles; 1 ♂ WN, Tararua Forest Park, Mt Hector, 4500–5000 ft, 15 Feb 1921, No. 168; 3 ♂ same range, above Dennan, 1300 m, beaten on *Dracophyllum*, 21 Dec 1987, A.C.E. (1 taken as 5th instar nymph and reared to adult); 1 ♂ 1 ♀ same data except J. I. Townsend.

Diagnosis. *R. russatus* n. sp. is distinguished from *R. gracilis* n. sp. by the red colour and presence of semi-erect hairs on clavus and near base of corium.

Distribution. An alpine species occurring from the Tararua Range in the North Island, through Nelson, Marlborough, Kaikoura, and North Canterbury in the north of the South Island.

Biology. Breeds on *Dracophyllum* as adults and 3rd–5th instar nymphs have been taken on it. Adults have also been taken on *Helichrysum selago*, *Cassinia vauvilliersii*, and tussock.

Remarks. A slender species with genitalia intermediate between the type and *R. rupestris* n. sp. The red colour of fresh field specimens tends to fade in collections.

Rhyodes sericatus Usinger
(Fig. 29–31, 144, 145, 162, 163)



Fig. 144 *Rhyodes sericatus* Usinger ♂.

Rhyodes sericatus Usinger 1942b: 46–47 (Original description; keyed).

Rhyodes sericatus: Slater 1964: 345 (Catalogue).

Rhyodes sericatus: Ashlock 1967: 56 (List).

Rhyodes sericatus: Wise 1977: 122 (List).

Characterised by the pale subapical corial spot (Fig. 144), spotted antennae, and paramere shape.

Colour. Black, brown, and pale; shiny. Head black, with a narrow orange stripe on edges of vertex; 1st antennal segment varies from dark, with pale base, to pale with dark spots; 2nd and 3rd segments mostly pale, with small brown spots, and with a narrow dark band at base; 4th segment dark, often light brown apically. Pronotum with posterior lobe pale except for brown posterior corners (sometimes with other brown areas). Scutellum usually with a mid-longitudinal pale stripe in apical half (varies from



Fig. 145 Distribution of *Rhyodes sericatus* Usinger.

completely black to completely pale except near base). Clavus and corium mottled with varying amounts of pale and brown; corium with a large pale subapical spot, and on basal side of it more brown markings across middle and on costal margin. Femora light yellow, with brown spots; tibiae pale, with small brown spots, and a black band near base.

Structure. Size: ♂ – length 4.45–5.50, width 1.6–2.0; ♀ – length 5.45–6.10, width 1.9–2.3. Form oval; connexivum usually slightly exposed in both sexes (rarely broadly exposed in ♀). Hemelytra with semi-erect hairs at base of clavus and corium only; fore tibiae with some long, outstanding hairs and some short hairs.

Head width to length 1.25 : 1.02 (1.35 : 1.05). Eye length 1.7× distance between anterior of eye and base of antenna, 0.37 : 0.22 (1.6×, 0.37 : 0.23). Width of vertex 3× eye width, 0.76 : 0.25 (0.80 : 0.27); vertex not elevated above eyes; juga not prominent. Antennal segments 0.42 : 0.88 : 0.70 : 0.74 (0.41 : 0.88 : 0.72 : 0.77); 1st segment with three-sevenths (♀ two-sevenths) of its length projecting beyond tip of tylus. Head in side view (Fig. 162) short and thick. Rostrum reaching mid coxae; 1st segment reaching base of head.

Pronotum width to length 1.75 : 1.10 (1.96 : 1.15); sides straightish to sinuate, not suddenly tapering anteriorly; punctuation on posterior lobe shallow, dense. Scutellum width to length 0.96 : 0.73 (1.10 : 0.82); apex rounded, upturned.

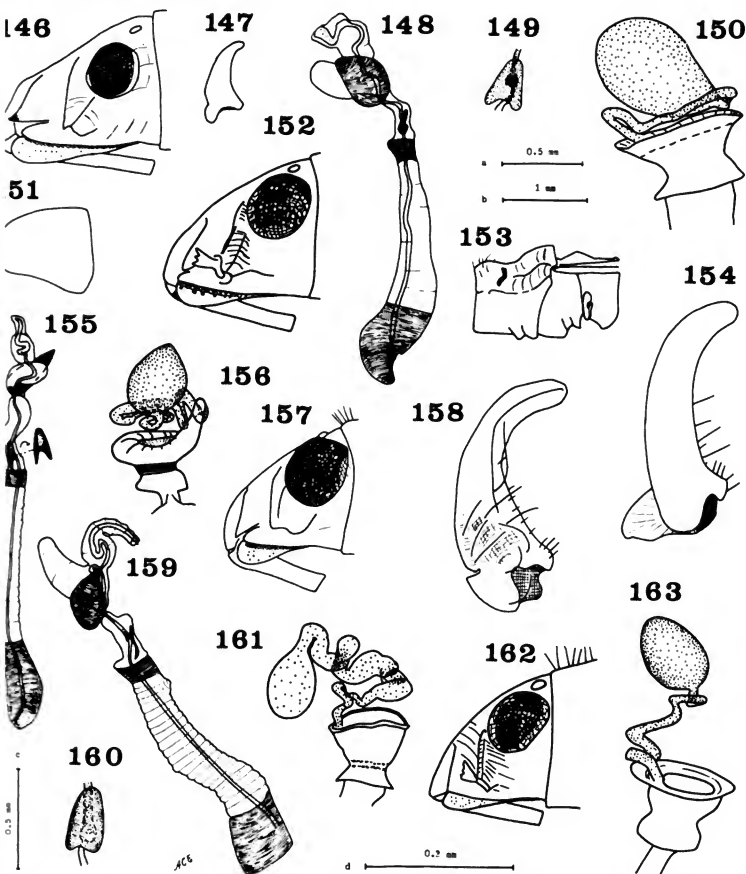


Fig. 146–163 146–151 *R. myersi*: 146, head, side view; 147, left paramere; 148, aedeagus; 149, ejaculatory reservoir (all ♂ Takitimu Ra.); 150, spermatheca; 151, ring sclerite (both ♀ Takitimu Ra.); 152–156 *R. rupestris* n. sp.: 152, head, side view; 153, thorax, side view; 154, left paramere; 155, aedeagus (all of paratype ♂); 156, spermatheca of paratype ♀; 157–161 *R. russatus* n. sp.: 157, head, side view; 158, left paramere; 159, aedeagus; 160, ejaculatory reservoir (all of holotype ♂ Mt Arthur); 161, spermatheca of paratype ♀ (Mt Arthur); 162–163 *R. sericatus*: 162, head, side view ♂ (Black Birch Ra.); 163, spermatheca ♀ (Mt Percival). Fig. 146, 147, 148, 152, 157, 162 to scale a; 149 to twice scale a; 153 to scale b; 155 to scale c; 150, 151, 154, 156, 158, 160, 161, 163 to scale d; 159 to half scale d.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft more than half as long as abdomen.

Genitalia. Paramere (Fig. 30) with blade long, broad, straight for part of its length, not tapering. Aedeagus (Fig. 31) with membranous lobes before sclerotised lobe on vesica; ejaculatory reservoir (Fig. 29) with A-shaped wings, neck attached to one side of frame.

Spermatheca (Fig. 163) with bulb lemon-shaped; flange with upper lip broad, flat.

Material examined. Holotype ♂ (5.33 × 2.00 mm), WN, Terawhiti, 23 Apr 1922, I.H.W. (USNM). Paratype ♂ same data as holotype except on *Cassinia* (CASC). Plus 75 specimens (CMNZ, FRNZ, NMNZ, NZAC).

Diagnosis. *R. sericatus* is distinguished from all other species of *Rhypodes* by the spotted antennae, and from *R. argenteus* n. sp. also by the mostly pale second antennal segment.

Distribution. A lowland and mountain species occurring from Kapiti Island, Plimmerton, and Wellington in the North Island, through D'Urville and Maud Islands in the Marlborough Sounds, through Mid Canterbury and the Mackenzie to Southland (Fig. 145). It is widespread in the South Island. Three other species occur in the South Island, but no further north than in and around Wellington. Although *R. sericatus* has been taken further north than *anceps* and *chinai* (and almost as far north as *R. russatus* n. sp.) its northern limit has yet to be established.

Biology. Breeds on *Helichrysum selago* as large numbers of adults and fifth instar nymphs were taken on and under this plant. A nymph, provided with *Helichrysum* seeds, was reared to an adult. It probably breeds on *Cassinia* also as adults have been taken in numbers in Marlborough on tauhinu (*Cassinia leptophylla*) and another species of *Cassinia*, and a specimen has been taken in Canterbury on *Cassinia fulvida*. Some live adults were found sheltering under speargrass (*Aciphylla*) and there were many dead adults between the layers of dead leaves under these plants at 4600 ft (1400 m) on Black Birch Range, Marlborough.

Remarks. Typical for sides of pronotum, but genitalia are as in *R. rupestris* n. sp. Colour varies, some specimens appearing darker (more grey) on the wings. The varying amount of pale and brown mottling may be an effect of the dense, silky white pubescence sometimes partly obscuring wing colour pattern.

Rhypodes spadix n. sp.
(Fig. 4, 5, 164, 165, 170–173)



Fig. 164 *Rhypodes spadix* n. sp. paratype ♂.

Characterised by the chestnut colour, origin of antennal tubercle in front of eye, and long, outstanding hairs on fore and mid tibiae.

Colour. Black and chestnut brown (Fig. 164); shiny. Head black; 1st and 4th antennal segments black (1st segment sometimes orange basally, 4th sometimes brownish orange at apex); 2nd and 3rd segments black or dark brown, with a narrow orange band at apex (sometimes with larger pale area in middle, and sometimes mostly pale except for dark base). Scutellum black, with an obscure mid-longitudinal orange stripe in apical half. Clavus and corium more or less uniformly chestnut brown; apex of corium dark; basal half of corium sometimes with small pale spots. Mid and hind femora spotted basally underneath; tibiae dark at base and apex.



Fig. 165 Distribution of *Rhyodes spadix* n. sp.

Structure. Size: ♂ – length 5.5–6.2, width 1.95–2.10; ♀ – length 5.6–7.0, width 2.15–2.65. Form al; connexivum usually exposed in ♀ (sometimes partly), unexposed in ♂. Hemelytra with semi-erect hairs well distributed, but short and bristly; for tibia (Fig. 4) with long, outstanding hairs; for tibia (Fig. 5) with a mixture of long, outstanding hairs and short hairs.

Head width to length 1.27 : 1.06 (1.37 : 1.09). Eye length 1.75× distance between anterior of eye and base of antenna, 0.40 : 0.23 (1.85×, 0.41 : 0.22). Width of vertex 2.7× eye width, 0.73 : 0.27 (2.75×, 0.30 : 0.29); vertex not elevated above eyes; jugal prominent. Antennal segments 0.42 : 0.83 : 0.65 : 0.31 (0.42 : 0.85 : 0.67 : 0.86); 1st segment with one-eighths (♀ one-third) of its length projecting beyond tip of tylus. Head in side view (Fig. 170) with antennal tubercle arising a little in front of eye; division of head between front of antennal tubercle and tip of tylus blunt (tilted down), and therefore shortened. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.73 : 1.07 (1.97 : 1.20); sides straightish, not suddenly tapering anteriorly; punctation on posterior lobe coarse, dense. Metellum width to length 1.01 : 0.80 (1.18 : 0.87); apex acute, upturned.

In ♀, abdominal sterna V and VI covered in middle; ovipositor cleft about half as long as abdomen.

Genitalia. Paramere (Fig. 171) with blade short, curved throughout, tapering. Aedeagus as in Fig. 172; vesica with the usual 2 ear-like lobes (1 sclerotised), and 2 or 3 more distal lobes; ejaculatory reservoir with broad wings.

Spermatheca (Fig. 173) with bulb elongate, lying over.

Type data. Holotype ♂ (5.88 × 2.00 mm), MK, Kea Walk, Mt Cook area, on *Hebe subalpina*, 7 Jan 1966, J. I. Townsend (NZAC). Allotype ♀ same data as holotype except A. C. Eyles (NZAC). Paratypes (19 ♂ 18 ♀; BMNH, NZAC, USNM): 9 ♂ 7 ♀ same data as holotype; 5 ♂ 5 ♀ same data as allotype; 3 ♂ 3 ♀ Kea Point track, The Hermitage, on *Hebe subalpina*, 7 Jan 1966, A.C.E.; 1 ♀ Kea Point track, Sealy Lake, bush sweep, 10 Jan 1966, A.C.E.; 1 ♂ 2 ♀ Mt Sebastopol, 2900 ft (884 m), on *Aciphylla aurea* flower, 8 Jan 1966, J.I.T.; 1 ♂ same data except 4800 ft (1464 m), on snowgrass, A.C.E.

Other material examined. 87 specimens (CMNZ, FRNZ, NMNZ, NZAC): NN, Mt Arthur, 4200 ft (1280 m), on *Hebe pauciramosa*, *Cassinia vauvilliersii*, *Cassinia* sp.; Spooners Range, 1800 ft, on *Hebe parviflora*; MB, Mt Curona, 3000 ft, on *Hebe odora*; Red Hills Plateau, 4500 ft; Jack's Pass, Hanmer; BR, Lewis Pass, 3500 ft; NC, Arthur's Pass, 3000–4000 ft; Mt Murchison, 4500 ft; on *Hebe odora*; MC, 4 ♂ 4 ♀ Mt Hutt, 3500 ft, on *Hebe*; Mt Somers, 2500 ft; MK, The Hermitage, 2500 ft; Hooker Valley, Kea Point; OL, Eyre Mts, 4000 ft, on *Cassinia*; Mt Dick, 1463 m; Bold Peak; Lake Wakatipu; CO, Kawarau Gorge, Roaring Meg, 488 m, adult and nymphs on *Hebe stricta*, B. M. May; Upper Manor Burn Reserve, sweeping tussock; DN, Lake Mahinerangi, 457 m, on *Hebe odora*; SL, Takitimu Mts, Tower Peak, 1067 m; Longwood State Forest; FD, Hunter Mts, S Borland River, 760 m, on *Olearia virgata* flower; 11 ♂ 10 ♀ Takahe Valley, on *Hebe*, A. C. Eyles and A. J. Saunders; Homer area, Lyttles Flat, on *Hebe*, once on *Olearia ilicifolia*.

Diagnosis. *R. spadix* n. sp. is distinguished from *R. longiceps* n. sp. by the antennal tubercle arising in front of eye (Fig. 170), the shorter and stouter appearing head, brown colour, and broader body.

Distribution. Occurs from 1500–4800 ft (457–1464 m) on mountain ranges throughout the South Island (Fig. 165).

Biology. Is associated with *Hebe* (five species) throughout its range. It breeds on this plant as many mating adults, and nymphs were taken on *Hebe subalpina* at the type locality, while in Central Otago adults with nymphs were taken on *Hebe stricta*. Also taken on *Cassinia*, *Olearia* (two species), and *Aciphylla aurea* (see Tables 3 and 4).

Remarks. Genitalia and sides of pronotum typical. Some specimens have a reddish tinge. The type series is limited to the fine series from the vicinity of The Hermitage.

***Rhyodes stewartensis* Usinger**
(Figs. 3, 34, 166, 167, 174–178)



Fig. 166 *Rhyodes stewartensis* Usinger holotype ♀.

Rhyodes stewartensis Usinger 1942b: 51–52 (Original description; keyed).

Rhyodes stewartensis: Slater 1964: 345 (Catalogue).

Rhyodes stewartensis: Ashlock 1967: 56 (List).



Fig. 167 Distribution of *Rhyodes stewartensis* Usinger.

Rhyodes stewartensis: Wise 1977: 122 (List).

Characterised by the widely spaced punctures on posterior pronotal lobe (Fig. 166), absence of semi-erect hairs on hemelytra, prominent juga which jut out from tylus, and robust, broad body for its short length.

Colour. Light brown, with faint mottling on wings; shiny. Head black, with a narrow pale stripe on edges of vertex; antennae black; 1st segment with pale base; 2nd and 3rd segments with a narrow pale band at apex (very narrow on 2nd segment). Pronotum with posterior lobe mainly pale. Scutellum black, with a mid-longitudinal pale stripe in apical one-third to half. Clavus and corium faintly mottled with variable amount of pale buff spots on brown; corium often mainly buff, with a few brown blotches. Femora with a yellow spot at apex; fore femora usually dark (sometimes spotted); mid and hind femora yellow, with black spots (which usually merge dorsally in apical half); tibiae yellow, with a dark band at apex and near base (Fig. 3).

Structure. Size: ♂ – length 4.65–5.45, width 1.75–2.30; ♀ – length 4.95–5.80, width 2.44–2.65. Form oval; connexivum partly exposed in many, but not

♀, usually unexposed in ♂. Lacking semi-erect on hemelytra.

Head width to length 1.3 : 1.0 (1.33 : 1.04). Eye gth 1.6× distance between anterior of eye and e of antenna, 0.37 : 0.23 (1.4×, 0.36 : 0.26). Width vertex 2.7× eye width, 0.73 : 0.27 (2.5×, 0.80 : 5); vertex not elevated above eyes; jugaprominent, distinctly separated, and jutting out, from tylus (Fig. 175). Antennal segments 0.45 : 0.8 : 0.6 : 0.8 (0.45 : 0.83 : 0.60 : 0.85); 1st segment with two-fifths to most half of its length projecting beyond tip of 2nd. Head in side view short and thick (Fig. 175), sum declivous. Rostrum reaching mid coxae; 1st ment reaching base of head.

Pronotum width to length 1.90 : 1.17 (2.14 : 1.4); sides straightish, not suddenly tapering anteriorly; punctation on posterior lobe coarse, widely spaced. Scutellum width to length 1.1 : 0.8 (1.28 : 1.4); apex acute, level.

In ♀, abdominal sternum VI covered in middle; posterior cleft less than half as long as abdomen (Fig. 34).

Genitalia. Paramere (Fig. 176) with blade short, curved throughout, tapering. Aedeagus (Fig. 177) with swelling of an outer membrane all round at base of conjunctiva; vesica with 3 small lobes (centre and one on each side) before 2 ear-like lobes; ejaculatory reservoir with broad, triangular wings.

Spermatheca (Fig. 178) with bulb elongate, lying anteriorly.

Material examined. Holotype ♀ (5.25 × 2.20 mm) Stewart Island, 1926, Harris (BMNH).

Paratype ♂ same data as holotype (CASC). Plus 63 specimens (NMNZ, NZAC). 3 ♀, 2 from West Arm, Lake Manapouri, under *Epilobium*, and 1 from Doubtful Sound, on *Senecio*, have been labelled with flow card "Rhyodes stewartensis Usinger 1942, compared with type, det. A. C. Eyles 1971" (NZAC).

Diagnosis. *R. stewartensis* is readily distinguished from *R. clavicornis* by the absence of pronotal angles, widely spaced pronotal punctures, declivous head, and broad, short body.

Distribution. Described from a male and female from Stewart Island, this species is distributed throughout the South Island, and has been taken in Wairarapa, Hawke's Bay, and Gisborne in the North Island (Fig. 167). A lowland and mountain species, occurring from sea level to 3800 ft (1160 m).

Biology. Breeds on *Epilobium pedunculare* as adults and nymphs of all stages were taken under isolated plants, and some nymphs reared through to adults on

the seeds. Often found under these plants in moist, gravelly areas such as creek beds, roadsides, or old quarries. It has also been taken under *Epilobium komarovianum*, *Spargula arvensis*, and *Gnaphalium luteo-album*, and on *Raoulia*, *Celmisia petrii*, and *Senecio*.

Remarks. Genitalia and sides of pronotum typical. I thought that *R. stewartensis* did not occur in the North Island, but as the study progressed some specimens were collected there. The similar, but hairy *R. brevifissus* n. sp. occurs in the North Island.

Rhyodes townsendi n. sp.

(Fig. 168, 179–182)

Characterised by the variegated wings (Fig. 168), deeply wrinkled dorsum of head, and broad, flattened body.

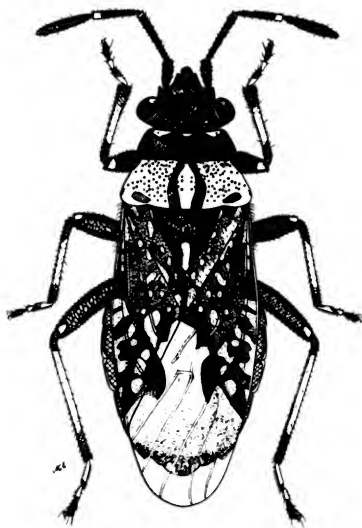


Fig. 168 *Rhyodes townsendi* n. sp. drawn from holotype ♀.

Colour. Variegated brown and buff; shiny. Head black; antennae black, with a narrow pale band at apex of 2nd and 3rd segments. Pronotum with a mid-longitudinal pale stripe and a brown stripe on each side; anterior margin with 3 pale spots; punctures brown. Scutellum black, with a mid-longitudinal pale stripe in apical half to two-thirds. Clavus and corium brown, variegated with small, pale buff spots. Femora black, with a small pale spot at apex; hind femora with other small, yellow spots; tibiae black at base and apex.

Structure. Size: ♂ – length 5.85, width 2.05; ♀ – length 6.8–7.2, width 2.45–2.55. Form oval; body flattened; connexivum broadly exposed (at least in ♀). Lacking semi-erect hairs on hemelytra.

Head width to length 1.35 : 1.15 (1.5 : 1.2). Eye length 1.6× distance between anterior of eye and base of antenna, 0.40 : 0.25 (1.5×, 0.45 : 0.30). Width of vertex 2.2× eye width, 0.70 : 0.32 (2.85×, 0.85 : 0.30); vertex not elevated above eyes; dorsum coarsely and deeply wrinkled; juga prominent. Antennal segments 0.45 : 0.95 : 0.70 : ? (0.45 : 0.95 : 0.80 : 0.90); 1st segment with one-third of its length projecting beyond tip of tylus. Head in side view (Fig. 179) appearing long and narrow. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.75 : 1.10 (2.15 : 1.30); sides straightish to slightly sinuate, not suddenly tapering anteriorly; punctuation on posterior lobe coarse, widely spaced. Scutellum width to length 1.00 : 0.85 (1.2 : 1.1); apex acute, level.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft half as long as abdomen.

Genitalia. Paramere (Fig. 181) with blade short, curved throughout, tapering; one edge serrated in basal half. Aedeagus (Fig. 180) with a prominent lobe near apex of conjunctiva; ejaculatory reservoir with broad, triangular wings.

Spermatheca (Fig. 182) with bulb elongate, lying over.

Type data. Holotype ♀ (6.80 × 2.55 mm), FD, Kaherekoau Mts, Lake Monowai, 4500 ft (1372 m), 29 Jan 1963, J. I. Townsend (NZAC). Allotype ♂ same data as holotype (NZAC).

Paratypes (2 ♀; AMNZ, NZAC): 1 ♀ same data as holotype; 1 ♀ OL, Minaret Peaks, Lake Wanaka, 27 Dec 1923, C. E. Clarke Collection, Lake Co, South Island.

Diagnosis. *R. townsendi* n. sp. is distinguished from *R. myersi* by the variegated wings, deeply wrinkled dorsum of head, flat vertex, and broad, flattened

body.

Distribution. A mountain species so far known from Fiordland and Otago Lakes.

Biology. Unknown.

Remarks. A large species, with sides of pronotum and genitalia typical. This remarkable species is named after my colleague Mr Ian Townsend who collected all but one of the type series, and also in recognition of his collecting work in the genus. He accompanied the author on many collecting trips in often remote and mountainous areas, and has collected or helped collect many of the new species.

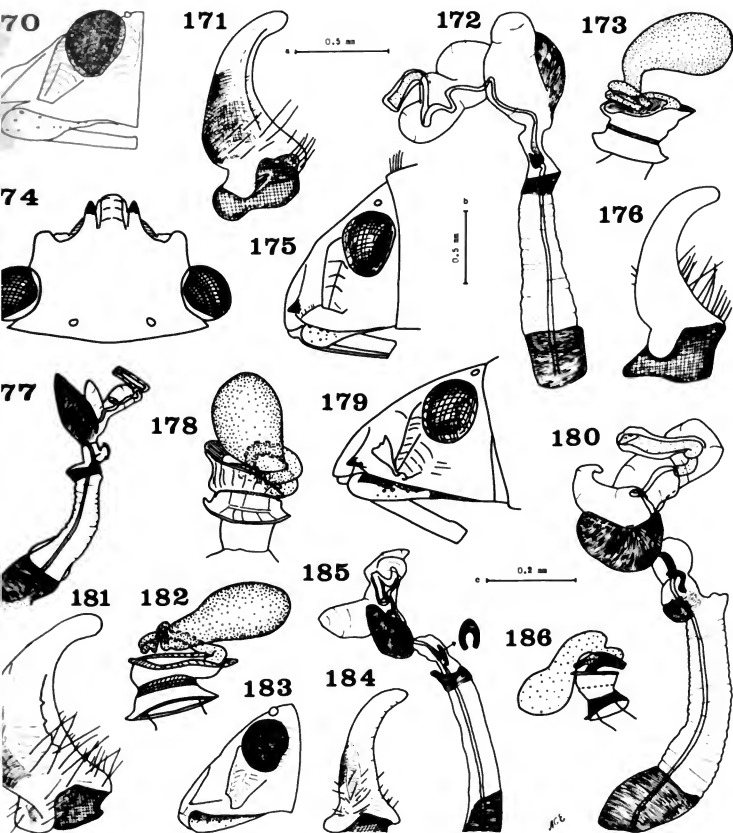
Rhyphodes triangulus n. sp.

(Fig. 169, 183–186)

Characterised by the pale subapical corial spot (Fig. 169), triangular plate-like projections on posterior margin of pronotum, and in particular, by the bright



Fig. 169 *Rhyphodes triangulus* n. sp. drawn from holotype ♂



170–186 170–173 *R. spadix* n. sp.: 170, head, side view; 171, left paramere; 172, aedeagus (all of paratype ♂); 173, spermatheca of paratype ♀; 174–178 *R. stewartensis*: 174, head, dorsal view; 175, head, side view (both ♀ Rahu and ♀ Idle); 176, left paramere; 177, aedeagus (both ♂ Manapouri); 178, spermatheca ♀ (Manapouri); 179–182 *R. townsendi* n. sp.: 179, head, side view of paratype ♀; 180, aedeagus; 181, left paramere (both of allotype ♂); 182, spermatheca of paratype ♀; 183–186 *R. triangulus* n. sp.: 183, head, side view; 184, left paramere; 185, aedeagus (all of paratype ♂ from more Hydro); 186, spermatheca of paratype ♀. Fig. 170, 177 to scale a; 174, 175, 179, 183 to scale b; 171, 173, 176, 181, 182, 184, 186 to scale c; 172, 180, 185 to half scale c.

yellow apical one-third of 3rd antennal segment, and yellow or light brown apex of 4th segment.

Colour. Mostly buff; shiny. Head black; 1st antennal segment black; 2nd segment brown, with a black band at base and a narrow yellow band at apex; 3rd segment brown, with a wide, bright yellow band at apex; 4th segment brown, with apex light brown, sometimes yellow; antenniferous tubercles black throughout. Pronotum pale buff except for black calli area, brown punctures, lateral margins, and a dark spot near posterior corners. Scutellum black, with a mid-longitudinal pale stripe in apical half, and lateral margins light brown in apical third. Clavus mostly buff except for brown streak on inner half of basal third. Corium mostly buff, with a pale subapical spot; apex, and a few blotches across middle, brown. Femora brown, with yellow apex; mid and hind femora yellow at base; tibiae yellow, with a brown band at apex and near base.

Structure. Size: ♂ – length 4.6–5.9, width 1.8–2.0; ♀ – length 5.4–6.1, width 1.95–2.05. Form oval; connexivum unexposed. Semi-erect hairs on dorsum of head near eyes only; lacking semi-erect hairs on hemelytra.

Head width to length 1.15 : 1.00 (1.20 : 1.07). Eye length 1.5× distance between anterior of eye and base of antenna, 0.35 : 0.23 (1.4×, 0.35 : 0.25). Width of vertex 2.5× eye width, 0.63 : 0.25 (2.8×, 0.70 : 0.25); vertex not elevated above eyes; juga not prominent. Antennal segments 0.40 : 0.90 : 0.55 : 0.65 (0.40 : 0.85 : 0.55 : 0.65); 1st segment with three-eighths of its length projecting beyond tip of tylus. Head in side view (Fig. 183) appearing long and narrow. Rostrum reaching hind coxae; 1st segment reaching base of head.

Pronotum width to length 1.70 : 1.04 (1.84 : 1.10); sides straightish, not suddenly tapering anteriorly; posterior margin with 2 large, triangular, plate-like projections overlapping bases of clavi (as in Fig. 89); punctuation on posterior lobe coarse, widely spaced. Scutellum width to length 1.00 : 0.77 (1.06 : 0.80); apex acute, level.

In ♀, abdominal sternum VI covered in middle; ovipositor cleft half as long as abdomen.

Genitalia. Paramere (Fig. 184) with blade shortish, horn-shaped. Aedeagus (Fig. 185) with subapical conjunctival sclerotised band extended on one side; vesica with 1 of the lobes large; ejaculatory reservoir A-shaped, with wings curving towards each other at base of A.

Spermatheca (Fig. 186) with bulb elongate, lying over.

Type data. Holotype ♂ (5.17 × 1.87 mm), MK, Benmore hydro road, 1500 ft (475 m), on *Raoulia* mats, 18 Jan 1966, J. I. Townsend (NZAC). Allotype ♀ same data as holotype (NZAC). Paratypes (5 ♂ 3 ♀; NMNZ, NZAC): 2 ♂ 1 ♀ same data as holotype; 2 ♂ 2 ♀ same data as holotype except 2000–3000 (610–915 m); 1 ♂ OL, Paradise Lake on Pigeon Island, Lake Wanaka, 30 Feb 1967, J. R. and J. V. Greenfield.

Diagnosis. *R. triangulus* n. sp. is similar to *R. chinai* in having triangular plate-like projections on posterior margin of pronotum and a pale subapical corial spot, but is distinguished from it by the bright yellow and often wider pale band on apex of third antennal segment, bright yellow hemelytra, only abdominal sternum VI covered in middle in females, and differences in the male genitalia.

Distribution. So far known only from Mackenzie and Otago Lakes.

Biology. Taken on, and probably lives on, *Raoulia*.

Remarks. Pronotum and genitalia typical.

PHENETIC ANALYSIS

A numerical study of the phenetic relationships among 27 of the 28 species in the genus was carried out. The decision to separate *R. cognatus* n. sp. from *R. clavicornis* was made after the phenetic analysis was run. A phenogram of males and females combined is presented, along with a 3-dimensional ordination graph based on the same similarity matrix, and the shortest minimally connected network amongst the species in the original space of distances. Separate phenograms for males and females are given to see if the phenetic similarities among the species are the same in the two sexes and in the combined one. These are for 26 species, as there are no females of *R. brevipilis* and, at the time of taking the measurements, no males of *R. crinitus*. In the combined phenogram and ordination there were 96 total characters. In the phenogram for males 70, and that for females 71, characters.

Tabulation of characters and scoring used

There were 23 quantitative characters for each sex = 46 characters, 17 present or absent characters, and 33 multistate characters.

Quantitative characters (Actual measurements, means):

- head length
- 1st antennal segment, length
- 2nd antennal segment, length
- 3rd antennal segment, length
- 4th antennal segment, length
- eye width
- vertex width
- distance between anterior margin of eye and tip of antennal tubercle
- eye length
- pronotum width
- pronotum length
- scutellum width
- scutellum length
- hind femur, length
- hind tibia, length
- body width
- 1st rostral segment, length
- 2nd rostral segment, length
- 3rd rostral segment, length
- 4th rostral segment, length
- membrane from base to level of apices of coria
- membrane from level of apices of coria to apex
- claval commissure, length

Present or absent characters (Scoring: 1 if present, 0 if absent; or 1 for one condition, 0 for the other):

- 1. bucculae: project anteriorly beyond tylus or not
- 2. bucculae: coarsely punctate or finely punctate
- 3. antennae spotted or not
- 4. presence or absence of pointed projections on side of pronotum at anterior
- 5. venter of antennal tubercle dark throughout, or with at least tip pale
- 6. whether hairs on anterior half of pronotum long or very long
- 7. whether pronotal sides suddenly tapering anteriorly (with well developed postero-lateral angles), or straightish and not suddenly tapering anteriorly
- 8. presence or absence of distinct sinuation on pronotum in side view, through different elevation of lobes
- 9. presence or absence of longish, silky, silvery pubescence
- 10. presence or absence of a pale subapical corial spot
- 11. whether pubescence extremely short or not
- 12. presence or absence of long hairs on edge of costal margin at base
- 13. membrane fully developed or reduced
- 14. whether femora spotted or not

- 38. whether tibiae spotted or not
- 39. presence or absence of lobe near apex of conjunctiva
- 40. whether posterior pronotal lobe pale throughout or not

Ordered multistate characters (Scoring: each state given successive increasing numbers 1, 2, 3, etc.):

- 41. body shape: oval, parallel sided, egg-shaped
- 42. elevation of vertex: mound, convex above eyes, flatter and not above top of eyes
- 43. long hairs on dorsum of head: present throughout, near eyes only, absent
- 44. juga: very prominent (wide gap between tylus and paraclypeal lobes), prominent (slight gap), not prominent (tips of paraclypeal lobes close to tylus)
- 45. colour of 1st antennal segment: black or dark throughout, black or dark with narrow pale base, all or mostly pale or orange
- 46. colour of 2nd antennal segment: black or dark throughout, black or dark with pale apical band, all or mostly pale or orange
- 47. colour of 3rd antennal segment: black or dark throughout, dark with narrow pale apical band, dark with wide pale apical band, all or mostly pale or orange
- 48. colour of 4th antennal segment: black or dark throughout, dark with orange or lighter apex, all or mostly pale or orange
- 49. colour of bucculae: all pale, pale with basal black stripe, all black or dark brown
- 50. colour of 1st rostral segment: dark throughout, dark with pale apex, all or mostly pale
- 51. 1st rostral segment reaches: before base of head, base of head, beyond base of head
- 52. rostrum reaches: mid coxae, hind coxae, beyond hind coxae
- 53. plate-like projections from posterior margin of pronotum overlapping bases of clavi: large and triangular, small and rounded, absent
- 54. punctuation on posterior pronotal lobe: coarse and dense, coarse and widely spaced, shallow and dense, shallow and widely spaced
- 55. long hairs on posterior half of pronotum: absent, present, very long
- 56. long hairs on scutellum: absent, present, very long
- 57. apex of scutellum: acute and level, acute and upturned, rounded and level, rounded and upturned
- 58. colour of scutellum: uniformly dark, pale spot on anterior arms only, pale longitudinal stripe

- apically, the previous two in combination, mostly red
59. wing length: macropterous, sub-brachypterous, brachypterous
 60. erect or semi-erect hairs on hemelytra: absent, at base of clavus and corium only, well distributed, very long
 61. R + M branch: at level of apex of scutellum, between there and middle of clavus, after middle and before apex of clavus, at apex of clavus, beyond apex of clavus
 62. relation of M to R on apical margin of corium: M nearer to Cu than to R, M equidistant from Cu and R, M nearer to R than to Cu
 63. colour of corium and clavus: uniformly pale, mottled, mixed with dark and pale areas, with pale stripe following costal margin, uniformly dark
 64. colour of coxae: dark throughout, apices pale, pale throughout
 65. fore femora: moderately swollen, medium, slender
 66. long hairs on fore femora (excluding ventral rows): absent, present, very long
 67. long hairs on mid and hind femora (excluding ventral rows): absent, present, very long
 68. long outstanding hairs on fore tibiae: absent, present, very long
 69. long outstanding hairs on mid and hind tibiae: absent, present, very long
 70. shape of parameres: *clavicornis*-like, *chinai*/*gracilis*-like, *anceps*-like, *clavicornis*-like with flatter blade, *rupestris*-like
 71. ovipositor cleft: more than half as long as abdomen, half as long as abdomen, less than half as long as abdomen
 72. sterna V and VI in females: both covered in middle, only VI covered in middle, both uncovered in middle
 73. spermatheca: bulb elongate and lying over, with long disorganised duct and intermediate bulb, bulb rounded, bulb round and duct very long

Analytical Method

The data were processed with a programme called ASSORT developed for the Elliot 503 computer at Applied Mathematics Division, DSIR, Wellington by Randal (1968), using options and extensions of the package incorporated by Dr J. H. Darwin and Mr J. M. O. Wood. The function for distance between two species was that in Gower (1971), except that all dichotomous variables with states 0 and 1 were assumed symmetrical, i.e. both (1, 0) and (0, 1) were

(1, 1) for two species being taken as indicating zero distance between the species for that variable.

The clustering method was to combine the two closest groups at any stage into a new group. The distance between the combination of old groups *i* and *j* and any other group *k* was taken as

$$\text{distance}((i, j) \text{ to } k) = .625 \times \text{distance}(i \text{ to } k) + .625 \times \text{distance}(j \text{ to } k) - .25 \text{ distance}(i \text{ to } j)$$

For the ordination, Gower's (1966) procedure was followed for a similarity matrix in which the (i, j) th element was $1 - (i, j)$ th element of the distance matrix.

The Prim network analysis (Prim 1957) was used for computing the shortest minimally connected network amongst the species in the original space of distances. It is presented as a table rather than superimposed on the ball and stick diagram to avoid confusion with too many lines.

Results

There is close agreement between the combined phenogram (Fig. 187), ordination (Fig. 188) and network (Table 2), and with the comments on groupings made in the section "Limits of the genus *Rhyphodes*". It is interesting that the phenogram showed the close similarity between *R. brevipes* and *R. bucculentus* before the author was aware of it.

The separate male (Fig. 189) and female (Fig. 190) phenograms agree in the first part *chinai* to *russatus* (or to *brachypterus*). However, just after that *argenteus* and *sericatus* are at the right hand end of the first main branch in males. *R. rupestris* and *eminens* are also in a different place. Apart from that the other groupings, *koebelii* to *clavicornis* to *jugatus*, and *myersi* to *depilis*, etc., more or less agree.

The phenograms of each sex show agreement with the combined one (Fig. 187) from *chinai* to *brachypterus* (right hand end). The middle branch of the combined one also agrees with the separate male and female groupings. Then *stewartensis* to *clavicornis* to *jugatus*, and the hairy species *brevifissus* and *hirsutus* are together in all three phenograms, though in a different place.

The cophenetic correlation between the distances between species in the original Gower matrix and the distances in the Gower 3-dimensional ordination is 0.924.

Conclusion: There is a fairly close agreement between the separate male and female phenograms and the combined one. There is closer agreement between the combined phenogram, ordination, and minimally connected network. The phenetic analysis results support the comments on groupings made under

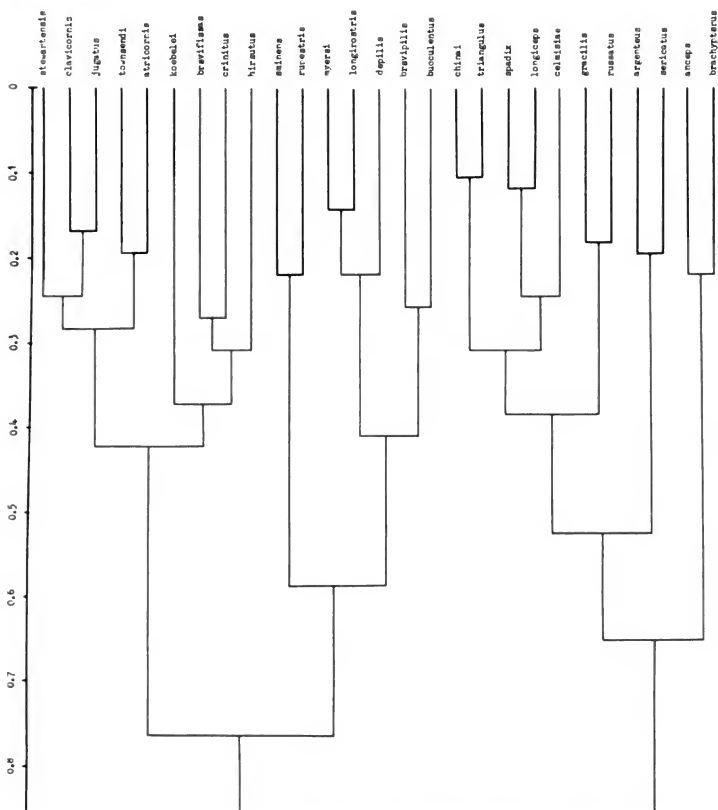


fig. 187 Distance phenogram of the genus *Rhyodes* males and females combined (excluding *R. cognatus*) based on 5 characters, computed from Gower's (1971) distance function and flexible sorting. The scale is distance.

remarks and elsewhere through the paper which are based on similarity in traditional taxonomic treatment.

BIOLOGY

Food

Considerably more information on feeding in *Rhyodes* has been brought to light in the present study, mainly from field observations, than was previously known. These bugs are seed feeders, getting nourishment from both developing seeds on the plants and ripened seeds on the ground under the plants. If necessary, these bugs would be able to sustain themselves for a short time on vegetative parts of plants, which also serve as a source of moisture. Food plants and plants on which the bugs were taken are tabulated in Table 3. Some are chance associations, the bugs merely resting there, although the true food plant may have been nearby.

Two-thirds of the species occur on various Compositae. Half of these occur on *Celmisia* species and one quarter each on *Raoulia* species and *Helichrysum* species. There is only one species for

which no host plant data is available. The remaining third occur on five other plant families. Three species occur on *Epilobium* (Onagraceae), two on *Dracophyllum* (Epacridaceae), two on *Hebe* (Scrophulariaceae), one on *Carex* (Cyperaceae), and one mainly on *Leptospermum* (Myrtaceae).

Four species, *clavicornis*, *myersi*, *longirostris*, and *hirsutus*, definitely breed on *Celmisia*. Adults have been taken on the plant and nymphs on and in the seedheads. Some 10–20 nymphs per seedhead of various instars were found feeding on the seeds, safely concealed beneath the parachute canopy. This should be sufficient evidence to safely conclude that the other four species consistently taken on *Celmisia*, namely, *R. celmisiae*, *longiceps*, *jugatus*, and *depilis*, also breed on these plants.

One species, *R. chinai*, definitely breeds on *Raoulia* mat plants as adults have been taken and observed mating on these plants (Myers 1926 as *Nysius* sp.; White 1969; and by the present author). Eggs are oviposited in the leaf axils (White 1969). In the present study, nymphs taken on this plant have been reared through to adults. As numbers of *R. argenteus*, *atricornis*, and *triangulus* are also taken from *Raoulia*, it seems reasonable to assume that they breed there as well.

Rhyodes rupestris and *R. sericatus* have been taken as adults and fifth instar nymphs under *Helichrysum* shrublets, and the nymphs reared through to adults on collected seedheads. As these two species feed and breed on this plant, it is reasonable to conclude that *R. eminens* and *R. brachypterus*, taken in numbers under *Helichrysum*, also breed on it. *R. rupestris* was found high up on a wind-swept scree under tiny shrublets, the only vegetation around for several metres.

Rhyodes stewartensis definitely breeds on *Epilobium* as adults and nymphs of all instars have been taken in numbers on and under several isolated plants in this genus. *R. brevifissas* and *R. bucculentus* have also been taken under *Epilobium*, the latter species under isolated plants on shingle scree.

Rhyodes russatus definitely breeds on *Dracophyllum* as adults and nymphs of several instars have been taken on it and some fifth stage nymphs reared to adults. *R. gracilis*, also a slender species, also breeds on this plant. It has been taken in equal numbers on and breeds on snowgrass—*Danthonia flavescens* (Gramineae).

Large numbers of *R. spadix*, including some nymphs and many mating adults, taken on *Hebe subalpina* indicate a definite association with this plant. *R. brevipilis* was taken on it in low numbers.

Table 2 Shortest minimally connected network amongst the species in the original space of distances.

Species linked		Length of link
<i>chinai</i>	<i>triangulus</i>	0.0987
<i>chinai</i>	<i>gracilis</i>	0.2269
<i>gracilis</i>	<i>russatus</i>	0.1829
<i>gracilis</i>	<i>rupestris</i>	0.2875
<i>rupestris</i>	<i>eminens</i>	0.2140
<i>anceps</i>	<i>brachypterus</i>	0.2211
<i>brachypterus</i>	<i>celmisiae</i>	0.3085
<i>celmisiae</i>	<i>longiceps</i>	0.1942
<i>longiceps</i>	<i>spadix</i>	0.1162
<i>longiceps</i>	<i>townsendi</i>	0.1762
<i>longiceps</i>	<i>argenteus</i>	0.2850
<i>argenteus</i>	<i>sericatus</i>	0.1897
<i>spadix</i>	<i>koebeli</i>	0.1984
<i>spadix</i>	<i>clavicornis</i>	0.2068
<i>clavicornis</i>	<i>stewartensis</i>	0.2036
<i>clavicornis</i>	<i>jugatus</i>	0.1621
<i>clavicornis</i>	<i>brevifissas</i>	0.2476
<i>brevifissas</i>	<i>crinitus</i>	0.2715
<i>townsendi</i>	<i>atricornis</i>	0.1965
<i>townsendi</i>	<i>hirsutus</i>	0.3208
<i>atricornis</i>	<i>myersi</i>	0.2197
<i>myersi</i>	<i>longirostris</i>	0.1464
<i>myersi</i>	<i>depilis</i>	0.1813
<i>depilis</i>	<i>brevipilis</i>	0.2599
<i>brevipilis</i>	<i>bucculentus</i>	0.2574

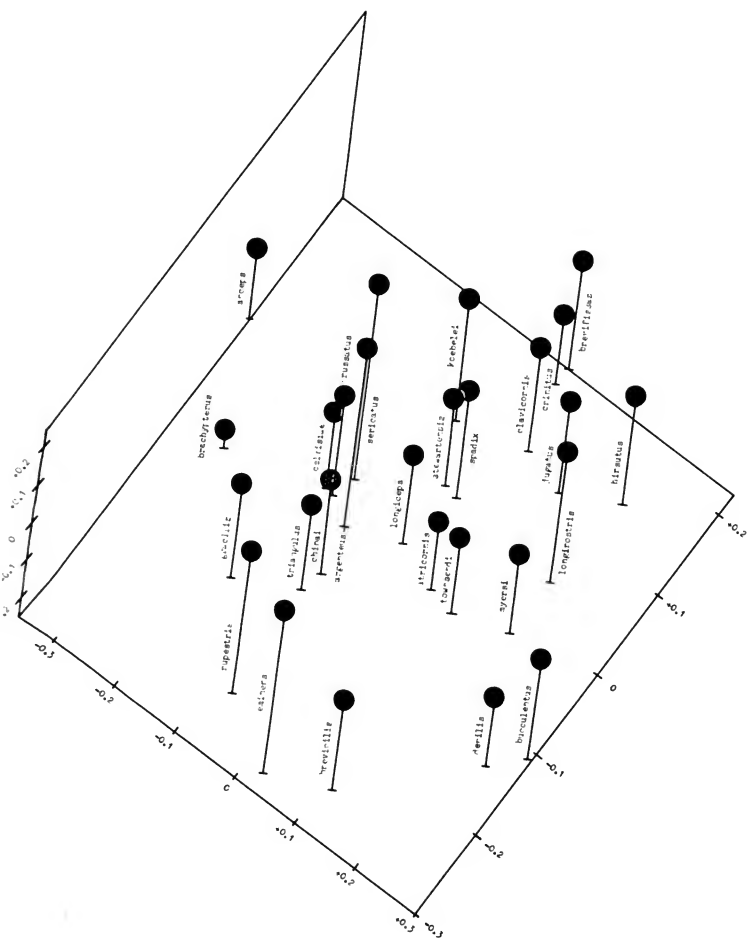


Fig. 188 Axonometric projection of 27 species of *Rhyopodes* on the first three principal components on the similarity matrix (Gower 1966). Height is to the bottom of the balls.

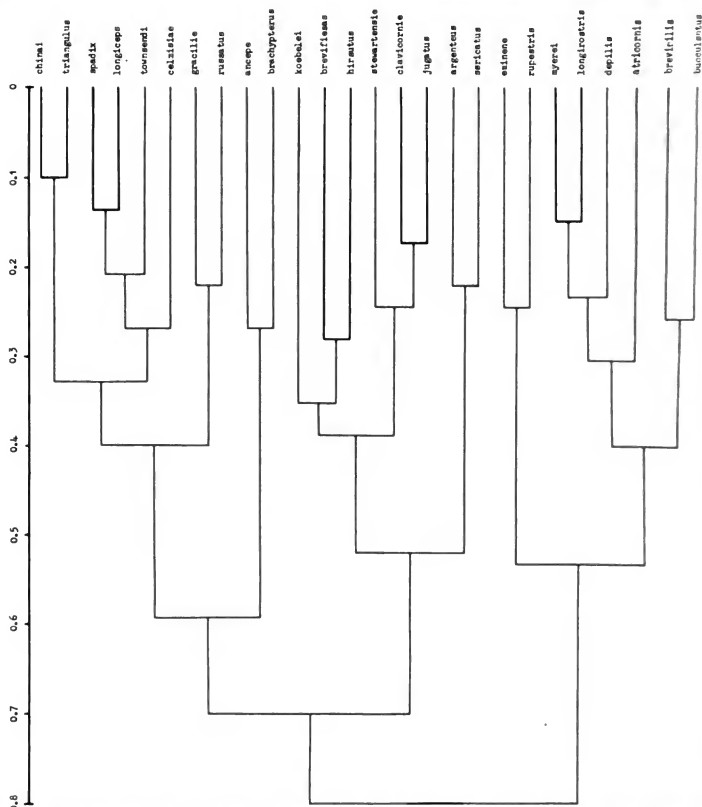


Fig. 189 Distance phenogram of males of the genus *Rhyodes* (excluding *R. cognatus* and *R. crinitus*) based on 70 characters, computed from Gower's (1971) distance function and flexible sorting. The scale is distance.

Two specimens of *R. crinitus* were swept from seedheads of the sedge *Carex solandri* (which had some grass around it, but sweeping was concentrated on the sedge). One specimen taken as a fifth instar nymph and provided with *Carex* seeds later moulted to an adult.

As several specimens of *R. koebeleri* have been taken on manuka flowers, this can be regarded as a

definite host association. Only single specimens have so far been taken on a number of other different plants.

Rhyodes clavicornis breeds on several other hosts in addition to *Celmisia*, most being Compositae. It has become well adapted to the introduced weed ragwort (*Senecio*) on which adults and nymphs occur in large numbers over a wide area. Large numbers

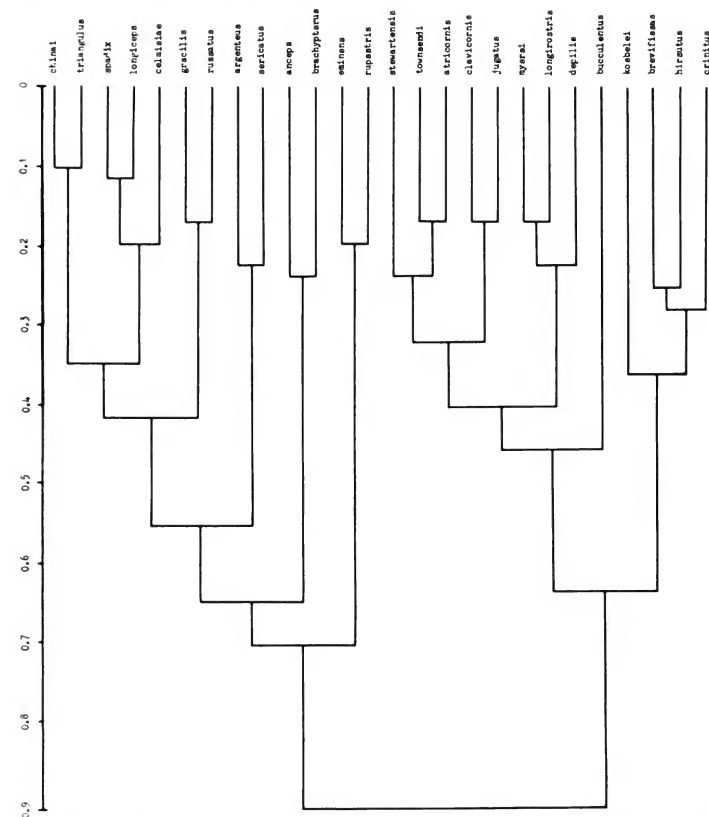


Fig. 190 Distance phenogram of females of the genus *Rhynchos* (excluding *R. brevipilis* and *R. cognatus*) based on 71 characters, computed from Gower's (1971) distance function and flexible sorting. The scale is distance.

have been taken on *Cassinia* and *Eupatorium* indicating a definite host association, and as I have taken it on three occasions on flowering manuka (Myrtaceae) in reasonable numbers, this cannot be discounted. Its collection in ones or twos on the composites *Cotula*, *Erechtites minima*, cudweed (*Gnaphalium*), dandelion (*Taraxacum*) yarrow lowers (*Achillea*), thistle, chrysanthemum, and

lettuce (not known if it had gone to seed) may indicate an ability to feed on a wide range of Compositae at least temporarily. It has been taken on *Nothofagus* on three occasions (seven specimens in one instance).

Rhynchos anceps, taken on a number of different species of plants (Table 3), has also become adapted to a wide range of hosts including introduced weeds.

Table 3 Food plants of species of *Rhynchospora* and plants on which specimens have been taken, showing plant family, part fed on (if known), author and new records.

Species	Family	Plant	Author
Previous records			
<i>anceps</i>	Gramineae	grasses ¹	Myers 1926
	Juncaceae	rushes ¹	Myers 1926
	Gramineae	wheat ⁴	Morrison 1939; Blair & Morrison 1949
	Gramineae	<i>Festuca novae-zelandiae</i> ⁵	Kelsey 1957
	Gramineae	<i>Poa caespitosa</i> ⁵	Kelsey 1957
	Gramineae	<i>Poa colensoi</i> ⁵	Kelsey 1957
<i>chinai</i>	Compositae	<i>Raoulia tenuicaulis</i> ¹	White 1969
	Gramineae	tall tussock ¹	White 1969
(as <i>Nysius</i> 2nd sp)	Umbelliferae	<i>Angelica montana</i> ²	Myers 1926 p. 481
<i>clavicornis</i>	Compositae	<i>Cassinia leptophylla</i> ²	Myers 1926; Eyles 1974
	Compositae	<i>Chrysanthemum</i> ²	Myers 1926
	Compositae	<i>Senecio jacobaea</i> ¹	Eyles 1974
	Myrtaceae	<i>Metrosideros scandens</i> ¹	Myers 1926
	Onagraceae	<i>Fuchsia excorticata</i> ¹	Myers 1926
	Gramineae	grasses ¹	Myers 1926; Woodward 1954
	Myrtaceae	<i>Kunzea ericoides</i> ¹	Woodward 1954
	Myoporaceae	<i>Myoporum laetum</i> ¹	Woodward 1954
	Gramineae	<i>Poa anceps</i> ^{1,3}	Woodward 1954
	Scrophulariaceae	<i>Hebe insularis</i> ¹	Woodward 1954
	Chenopodiaceae	<i>Chenopodium triandrum</i> ¹	Woodward 1954
	Haloragaceae	<i>Haloragis erecta</i> ¹	Woodward 1954
	Cyperaceae	<i>Scirpus</i> ¹	Woodward 1954
	Cyperaceae	<i>Carex</i> ¹	Woodward 1954
	Cyperaceae	sedges ¹	Woodward 1954
	Juncaceae	rushes ¹	Woodward 1954
	Azaceae	<i>Tetragonia</i> ¹	Woodward 1954
<i>myersi</i>	Compositae	<i>Celmisia</i> spp. ¹	Eyles 1974
<i>sericatus</i>	Compositae	<i>Cassinia leptophylla</i> ¹	Usinger 1942b
New records			
<i>anceps</i>	Compositae	<i>Celmisia spectabilis spectabilis</i> ¹	
	Compositae	<i>Celmisia prorepens</i> ¹	
	Compositae	<i>Raoulia tenuicaulis</i> ¹	
	Compositae	<i>Raoulia</i> sp. ¹	
	Compositae	<i>Haastia pulvinaris</i> ²	
	Polygonaceae	<i>Rumex acetosa</i> ⁴	
	Polygonaceae	<i>Muehlenbeckia</i> ¹	
	Onagraceae	<i>Epilobium porphyrium</i> ³	
	Gramineae	<i>Chionochloa macra</i> ¹	
	Gramineae	<i>Danthonia flavescens</i> ¹	
	Epacridaceae	<i>Dracophyllum muscoides</i> ¹	
	Umbelliferae	<i>Aciphylla squarrosa</i> ³	
	Ranunculaceae	<i>Ranunculus</i> ²	
	Scrophulariaceae	<i>Hebe subalpina</i> ¹	
<i>argenteus</i> n. sp.	Compositae	<i>Raoulia</i> ¹	
<i>atricornis</i> n. sp.	Compositae	<i>Raoulia tenuicaulis</i> ¹	
	Onagraceae	<i>Epilobium pedunculare</i> ³	
<i>brachypterus</i> n. sp.	Compositae	<i>Helichrysum</i> ³	
	Umbelliferae	<i>Aciphylla</i> ³	
	Ranunculaceae	<i>Ranunculus</i> ²	
<i>brevifissus</i> n. sp.	Onagraceae	<i>Epilobium komarovianum</i> ³	
<i>brevipilis</i> n. sp.	Scrophulariaceae	<i>Hebe subalpina</i> ¹	
<i>bucculentus</i> n. sp.	Onagraceae	<i>Epilobium pycnostachyum</i> ¹	
<i>celmisiae</i> n. sp.	Compositae	<i>Celmisia prorepens</i> ¹	
	Compositae	<i>Celmisia</i> ¹	
	Compositae	<i>Raoulia</i> ¹	

(continued)

Table 3 (continued)

Species	Family	Plant
<i>chinai</i>	Gentianaceae	<i>Gentiana bellidifolia</i> ¹
	Gramineae	grass ¹
	Compositae	<i>Raoulia australis</i> ¹
	Compositae	<i>Raoulia haastii</i> ¹
	Compositae	<i>Celmisia semicordata semicordata</i> ¹
	Compositae	<i>Celmisia spectabilis spectabilis</i> ¹
	Compositae	<i>Cassinia</i> ¹
	Compositae	<i>Olearia virgata</i> ¹
	Compositae	<i>Dolichoglottis scorzoneroideis</i> ¹
	Compositae	<i>Ilaestia pulvinaris</i> ¹
<i>clavicornis</i>	Umbelliferae	<i>Aciphylla</i> ¹
	Gramineae	<i>Chionochloa</i> ¹
	Gramineae	tussock ¹
	Polygonaceae	<i>Muehlenbeckia</i> ³
	Compositae	<i>Celmisia spectabilis spectabilis</i> ⁴
	Compositae	<i>Eupatorium riparium</i> ¹
	Compositae	<i>Eupatorium</i> sp. ¹
	Compositae	<i>Erechtites minima</i> ¹
	Compositae	<i>Gnaphalium collinum</i> ¹
	Compositae	<i>Senecio</i> ¹
	Compositae	<i>Cassinia retorta</i> ¹
	Compositae	<i>Achillea millefolium</i> ²
	Compositae	<i>Cotula</i> ¹
	Compositae	<i>Taraxacum officinale</i> ¹
	Compositae	<i>Lactuca sativa</i> ¹
	Compositae	thistle ¹
	Compositae	<i>Brachyglottis repanda</i> ²
	Umbelliferae	parsnip ¹
	Myrtaceae	<i>Leptospermum scoparium</i> ²
	Fagaceae	<i>Nothofagus menziesii</i> ¹
	Fagaceae	<i>Nothofagus</i> sp. ¹
	Epacridaceae	<i>Dracophyllum</i> ¹
	Papilionaceae	<i>Carmichaelia</i> ¹
	Leguminosae	broom ²
	Violaceae	<i>Hymananthera</i> ¹
	—	ferns ¹
<i>cognatus</i> n. sp.	Gramineae	silver tussock ¹
	Gramineae	tussock ¹
	Compositae	<i>Cassinia leptophylla</i> ¹
	Compositae	<i>Cassinia vauvilliersii</i> ¹
	Compositae	<i>Senecio jacobaea</i> ¹
	Compositae	<i>Sonchus oleraceus</i> ¹
	Compositae	<i>Olearia angustifolia</i> ²
	Compositae	<i>Olearia virgata</i> ¹
<i>crinitus</i> n. sp.	Compositae	<i>Brachyglottis repanda</i> ²
<i>depilis</i> n. sp.	Cyperaceae	<i>Carex solandri</i> ⁴
	Compositae	<i>Celmisia coriacea</i> ¹
	Compositae	<i>Senecio</i> ¹
<i>eminens</i> n. sp.	Gramineae	tussock ¹
	Compositae	<i>Helichrysum coralloides</i> ¹
<i>gracilis</i> n. sp.	Compositae	<i>Helichrysum selago</i> ¹
	Epacridaceae	<i>Dracophyllum</i> ⁴
<i>hirsutus</i> n. sp.	Gramineae	<i>Danthonia flavescens</i> ¹
	Compositae	<i>Celmisia spectabilis spectabilis</i> ⁴
	Compositae	<i>Senecio bidwillii</i> ⁴
	Compositae	<i>Olearia nummularifolia</i> ²
	Compositae	<i>Raoulia</i> ¹

(continued)

Table 3 (continued)

Species	Family	Plant
	Scrophulariaceae	<i>Hebe salicifolia</i> ²
	Scrophulariaceae	<i>Hebe odora</i> ¹
	Cyperaceae	<i>Uncinia rubra</i> ³
	Gramineae	tussock ¹
<i>jugatus</i> n. sp.	Compositae	<i>Celmisia semicordata semicordata</i> ¹
	Compositae	<i>Celmisia spectabilis spectabilis</i> ¹
	Compositae	<i>Cassinia</i> ¹
	Compositae	<i>Leucogenes grandiceps</i> ²
	Ranunculaceae	<i>Ranunculus lyalli</i> ²
<i>koebelei</i> n. sp.	Myrtaceae	<i>Leptospermum scoparium</i> ²
	Myrtaceae	<i>Kunzea ericoides</i> ¹
	Myrtaceae	<i>Metrosideros excelsa</i> ²
	Gramineae	grasses ¹
	Rosaceae	<i>Rubus australis</i> ¹
	Fagaceae	<i>Nothofagus menziesii</i> ¹
	Piperaceae	<i>Macropiper excelsum</i> ¹
	—	<i>Polygala myrrifolia</i> *. ¹
	Leguminosae	<i>Medicago sativa</i> ¹
	Iridaceae	<i>Gladiolus</i> sp. ¹
<i>longiceps</i> n. sp.	Compositae	<i>Celmisia semicordata stricta</i> ¹
	Compositae	<i>Celmisia petrii</i> ¹
	Compositae	<i>Celmisia</i> sp. ¹
	Gramineae	grass ¹
	—	<i>Cassinia</i> + <i>Dracophyllum</i> , sweep
<i>longirostris</i> n. sp.	Compositae	<i>Celmisia spectabilis spectabilis</i> ⁴
<i>myersi</i>	Compositae	<i>Celmisia spectabilis spectabilis</i> ⁴
	Compositae	<i>Celmisia semicordata semicordata</i> ⁴
	Compositae	<i>Celmisia semicordata stricta</i> ⁴
	Compositae	<i>Celmisia dalli</i> ⁴
	Compositae	<i>Celmisia sessiliflora</i> ⁴
	Compositae	<i>Celmisia</i> sp. ⁴
	Compositae	<i>Cassinia leptophylla</i> ¹
	Compositae	<i>Cassinia</i> sp. ¹
	Compositae	<i>Helichrysum coralloides</i> ³
	Umbelliferae	<i>Aciphylla</i> ¹
	Polytrichaceae	<i>Polytrichum</i> moss ¹
<i>rupestris</i> n. sp.	Compositae	<i>Helichrysum coralloides</i> ⁴
<i>russatus</i> n. sp.	Epacridaceae	<i>Dracophyllum</i> ⁴
	Compositae	<i>Helichrysum selago</i> ¹
	Compositae	<i>Cassinia vauvilliersii</i> ¹
	Gramineae	tussock ¹
<i>sericatus</i>	Compositae	<i>Cassinia fulvida</i> ¹
	Compositae	<i>Cassinia</i> sp. ¹
	Compositae	<i>Helichrysum selago</i> ⁴
	Umbelliferae	<i>Aciphylla</i> ³
<i>spadix</i> n. sp.	Scrophulariaceae	<i>Hebe subalpina</i> ⁴
	Scrophulariaceae	<i>Hebe stricta</i> ⁴
	Scrophulariaceae	<i>Hebe odora</i> ¹
	Scrophulariaceae	<i>Hebe parviflora</i> ¹
	Scrophulariaceae	<i>Hebe pauciramosa</i> ¹
	Umbelliferae	<i>Aciphylla aurea</i> ²
	Gramineae	<i>Danthonia flavescens</i> ¹
	Gramineae	tussock ¹
	Compositae	<i>Cassinia vauvilliersii</i> ¹
	Compositae	<i>Cassinia</i> sp. ¹
	Compositae	<i>Olearia ilicifolia</i> ¹
	Compositae	<i>Olearia virgata</i> ²

(continued)

Table 3 (continued)

Species	Family	Plant
<i>stewartensis</i>	Onagraceae	<i>Epilobium pedunculare</i> ⁴
	Onagraceae	<i>Epilobium komarovianum</i> ⁴
	Caryophyllaceae	<i>Spargula arvensis</i> ³
	Compositae	<i>Gnaphalium luteo-album</i> ³
	Compositae	<i>Senecio</i> ¹
	Compositae	<i>Raoulia</i> ¹
<i>triangulus</i> n. sp.	Compositae	<i>Celmisia petrii</i> ¹
	Compositae	<i>Raoulia</i> ¹

¹taken on plant; ²taken on flowers; ³taken under plant; ⁴feeds on seeds; ⁵feeds on leaves; ⁶taken on seedhead.

*label not clear.

As adults and nymphs were taken on roadside grass and weeds, notably sorrel (Polygonaceae), they were rearing there.

Habitat

Members of the genus occur in extremes of habitat from sea level to 1982 m (6500 ft) or more. Information, mainly from specimen labels, is presented in Table 4. Most of the species of *Rhyodes* occur on mountain ranges. Many may be taken on various species of *Celmisia* which grow in tussock grassland, herbfield, and fellfield. A few species may be found under *Helichrysum* in exposed situations high up (1524 m) on shingle screes. Species occurring on *Cassinia* and *Raoulia* are found at medium and lower altitudes, those on *Raoulia* often near creeks and in riverbeds. Species associated with *Epilobium* may be found at fairly high altitudes (1160 m) on shingle screes, or at medium and low altitudes near creeks or other moist, gravelly areas such as roadsides. Some species are taken in general beating in bush and some by sweeping in grass clearings and tussock. *R. celmsiae* has been taken in numbers on grass swards by a mountain stream.

Rhyodes clavicornis seems to be a low level and medium to high altitude species, whereas *R. koebeli* is a lowland species. *R. stewartensis* is both a low level and mountainous species, and so is *R. anceps*, which seems to have become adapted to feeding on roadside weed seeds.

Two species, *R. myersi* and *R. sericatus*, have been taken by me in large numbers under and between dead leaves of speargrass, *Aciphylla* (Umbelliferae), as well as some on the plant. Many dead adults of *sericatus* were found there between layers of dead leaves. This would provide good shelter during

winter, and the seeds of this plant must surely be a good food source. One specimen of *R. clavicornis* has been taken in dead kiekie (*Freycinetia*) in September (Myers 1926) and one under rotten bark of *Pseudopanax*, both perhaps overwintering sites. Hibernating adults of *R. anceps* were found under blue-gum bark (Myers 1926), and this species and *R. myersi* have been taken in debris under tussock.

Behaviour

If fast enough, one may catch *Rhyodes* on the plant with the hands, but they move to the underside of a leaf and quickly drop to the ground where there is protection in grass or debris or under stones. On *Celmisia* and *Aciphylla* they often move to shelter in the narrow space between the base of leaf and stem or between bases of leaves.

Rhyodes clavicornis taken on *Cassinia* and kept in tubes with flowering sprigs, laid eggs in the *Cassinia* flowers with the micropyle end upwards. Some flowering sprigs of sow thistle had also been put in and some eggs were laid in these flowers. Flowers were the chosen oviposition site, not other parts of the plant and not the cottonwool plug to the tube. However, females of *R. cognatus* taken on sow thistle in Nelson, laid eggs in the cottonwool plug and not in the sow thistle flowers.

Life history

Life histories of *Rhyodes* have not been studied in detail. Myers (1926) reported that adults of *anceps* and *clavicornis* overwinter. White (1969) described the egg and oviposition site of *chinai* and reported that eggs collected in the field hatched in 10 days from the time of collection. He also noted several specimens of a mite species on the coxae of adult females.

Table 4 Habitat of species of *Rhyodes* including previous and new records.

Species	Habitat	Author
Previous records		
<i>anceps</i>	Hibernating under bark of bluegum; swept from grasses and rushes.	Myers 1926
<i>chinai</i>	In wheat crops and weeds at edge of crop. Mt Matthews 3000 ft, Arthur's Pass 3800 ft. In Sep. clustered in thousands beneath stones and wood at 3000 ft. In Nov. swarming and mating on flowering <i>Raoulia tenuicaulis</i> .	Morrison 1939; Blair & Morrison 1949 Usinger 1942b Myers 1926 p. 481 (as 2nd <i>Nysius</i> sp.); White 1969
<i>clavicornis</i>	Hibernating in dead kiekie (<i>Freyinetia</i>). Often found on ragwort and tauhinu.	Myers 1926 Eyles 1974
<i>myersi</i>	Abundant on <i>Celmisia</i> flowers day and night.	Myers 1926 p. 481 (as 3rd <i>Nysius</i> sp.); Eyles 1974
<i>sericatus</i>	Common on tauhinu near Wellington.	Myers 1926, p. 481 (as 1st <i>Nysius</i> sp.); Usinger 1942b
New records		
<i>anceps</i>	Taken in large numbers sweeping tussock on Stephen's I., on ground with thin grass cover and high up on tall bracken (Kaikoura Ra.), on <i>Celmisia</i> spp., <i>Raoulia</i> mat plants and under <i>Epilobium</i> on mountains, and under weeds and grass on roadsides.	
<i>argenteus</i> n. sp.	On <i>Raoulia</i> mat plants.	
<i>atricornis</i> n. sp.	On <i>Raoulia</i> on scree above Takahe Valley; under <i>Epilobium</i> on Wilmot Pass.	
<i>brachypteris</i> n. sp.	Under <i>Helichrysum</i> on Mt Arthur.	
<i>brevifissas</i> n. sp.	Under <i>Epilobium</i> growing on stones by mountain creek.	
<i>brevipilis</i> n. sp.	On <i>Hebe subalpina</i> near The Hermitage.	
<i>bucculentus</i> n. sp.	On <i>Epilobium pycnostachyum</i> on scree 3800 ft, Mt Hutt; under stones Wairau V.	
<i>celmisiae</i> n. sp.	Montane on <i>Celmisia</i> spp., sometimes swarming on grass by a stream, sometimes on mat plants or sheltering under stones.	
<i>chinai</i>	Taken on <i>Celmisia</i> spp. and other Compositae, occasionally by sweeping tussock or on tussock at night, or sheltering under stones near mat plants.	
<i>clavicornis</i>	Taken from sea level to 6200 ft on <i>Celmisia spectabilis</i> on mountains and on ragwort in open grassland. Also associated with <i>Eupatorium</i> , manuka and possibly <i>Nothofagus</i> . Taken on several other Compositae, and at night on silver tussock. Found sheltering in dead leaves of <i>Dacrydium cupressinum</i> and under rotten bark of <i>Pseudopanax colensoi</i> .	
<i>cognatus</i> n. sp.	Taken sweeping tussock on Stephen's I., sweeping grass and weeds at Ship Cove, on sow thistle in Nelson and beating <i>Olearia angustifolia</i> flowers on Cofish I. Also taken on <i>Cassinia</i> spp.	
<i>crinitus</i> n. sp.	Taken sweeping grass and <i>Carex</i> on Mt Maungapohatu.	
<i>depilis</i> n. sp.	Found on <i>Celmisia coriacea</i> near Head Basin, Takahe Valley.	
<i>eminens</i> n. sp.	High up on the slopes of Mts Percival and St Patrick on <i>Helichrysum coralloides</i> and <i>Helichrysum selago</i> .	
<i>gracilis</i> n. sp.	Found on snowgrass and <i>Dracophyllum</i> .	
<i>hirsutus</i> n. sp.	Taken on mountains on <i>Senecio bidwillii</i> and <i>Celmisia spectabilis</i> .	
<i>jugatus</i> n. sp.	Found on <i>Celmisia</i> species.	
<i>koebelei</i> n. sp.	A lowland species found usually on flowering manuka and sometimes on kanuka. Also taken sweeping grass near bush.	
<i>longiceps</i> n. sp.	1000–5000 ft on <i>Celmisia</i> spp. and sheltering under stones. Sometimes taken in general beating, sweeping grassland, and on <i>Cassinia</i> and/or <i>Dracophyllum</i> .	
<i>longirostris</i> n. sp.	Abundant on <i>Celmisia spectabilis</i> on Mt Arawhano.	
<i>myersi</i>	Sometimes taken on <i>Cassinia</i> spp. Large numbers shelter in dead leaves under speargrass and some occur on the plant.	
<i>rupestris</i> n. sp.	On windblown scree at 1463 m under shrublets of <i>Helichrysum coralloides</i> .	
<i>russatus</i> n. sp.	On mountains, associated with <i>Dracophyllum</i> , but has also been taken on <i>Cassinia</i> , <i>Helichrysum</i> and tussock.	
<i>sericatus</i>	Abundant on and under <i>Helichrysum selago</i> . Also taken on 2 spp. of <i>Cassinia</i> in addition to tauhinu. Live adults shelter under speargrass and many dead adults were found there between layers of dead leaves.	
<i>spadix</i> n. sp.	Beaten in numbers with nymphs from <i>Hebe subalpina</i> ; taken on 4 other <i>Hebe</i> spp. Also taken on <i>Cassinia</i> and sometimes <i>Olearia</i> and <i>Aciphylla</i> .	
<i>stewartensis</i>	Adults and nymphs found on and under <i>Epilobium</i> on roadsides, creek beds, old quarries. Sometimes shelters under stones under these plants. Some adults found under spurry and some on <i>Raoulia</i> mats.	
<i>townsendi</i> n. sp.	Kaherekoau Mts (Lake Monowai) and Minaret Peaks (Lake Wanaka).	
<i>triangulus</i> n. sp.	On <i>Raoulia</i> mat plants.	

In the present study, eggs of *clavicornis* oviposited aptively and monitored during a field trip, hatched about 15 days, the first nymphal instar (on *Senecio* ds) lasting about 9 days.

There are five nymphal instars, the life history ng similar to those of *Nysius coenosulus* Stål 1859 l *Oceanides nubicola* Kirkaldy 1910, and *Nysius toni*, studied and figured, respectively, by Usinger 42a) and Eyles (1960a, 1963, 1974). As well as its, it is probable that some *Rhyodes* nymphs rwinter.

mpetition and zoning?

e day's collecting on Coronet Peak produced e closely related species on *Celmisia*: *R. myersi*, ich here seemed to be restricted to the lower pes, with *R. celmisiae* and *R. longiceps* higher up l at the summit. This is interesting because on other untains where the last two species have so far not n found, *myersi* has been taken at high levels as ll as on the lower slopes. Competition on Coronet ak may have caused this zoning, but this warrants ther investigation.

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Additions to the Chironomidae (Diptera: Insecta) of New Zealand: *Cricotopus* van der Wulp species from a North Island stream

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Abstract Two new species of *Cricotopus* (*Cricotopus*) van der Wulp are described in all life stages. Only three species of *Cricotopus* have previously been described from New Zealand: *C. zealandicus* Freeman, *C. cingulatus* Hutton, and *C. aucklandensis* Sublette & Wirth. Adult *Cricotopus vincenti* can be distinguished from *C. zealandicus* and *C. cingulatus* by a lack of tibial and abdominal markings, and from *C. aucklandensis* by a much higher antennal ratio, more anteprenotal setae, and a more distinct flange on the gonostylus. *C. planus* can be separated from *C. zealandicus* by a lack of pale tibial rings, and from *C. vincenti* and *C. aucklandensis* by the presence of abdominal markings. It is similar to *C. cingulatus* but can be distinguished by the small, low, and flattened inferior volsella, whereas *C. cingulatus* has a clearly pronounced and posteriorly-directed inferior volsella. The pupa of *C. planus* can be distinguished from that of *C. vincenti* and *C. aucklandensis* by the lack of a thoracic horn, and abdominal shagreen patterns. *C. vincenti* pupae can be separated from *C. aucklandensis* by the non-clubbed thoracic horn and abdominal shagreen patterns. The larva of *C. vincenti* is distinct from *C. planus* by its larger size, mentum

morphology, and the lack of any distinctive notch opposite the seta subdentalis in the mandible, and from *C. aucklandensis* by mentum characteristics. Comments are made on the life cycles of each species and affinities with the overseas fauna are discussed.

Keywords Chironomidae; Diptera; Insecta; *Cricotopus*; streams; systematics

INTRODUCTION

The New Zealand chironomid fauna has received little attention despite its abundance and importance in freshwater ecosystems (Leader 1975). Freeman (1959) reviewed the family but described only adults; apart from Brundin's (1966) major work on the Podonominae and Heptaglyiae only Forsyth (1971, 1975, 1979), Forsyth & McCallum (1978), and Leader (1975) have contributed to our knowledge. Sublette & Wirth (1980) described a number of new species from New Zealand's subantarctic islands, but most of these have yet to be found on the mainland. A recent development has been a key to the known chironomid larvae (Stark 1981). However, the Orthoclaadiinae, a subfamily predominant in lotic environments, is still poorly known.

As part of a study of lotic chironomids in the Waikato region, North Island, New Zealand (Boothroyd 1987), it has been necessary to investigate the taxonomy of several taxa. This paper presents descriptions of two new species of *Cricotopus*, one of the larger genera of the Orthoclaadiinae, and found in all zoogeographic regions of the world except Antarctica (Coffman et al. 1986). Only three species have previously been recorded from New Zealand: *Cricotopus zealandicus* Freeman, *C. cingulatus* Hutton, and *C. aucklandensis* Sublette & Wirth, but only the immature stages of *C. aucklandensis* are known (Boothroyd 1989).

In his major work on west palaearctic *Cricotopus* species, Hirvenoja (1973) considered the genus and its nearest relatives, *Acricotopus* Kieffer,

Paratrichocladius Santos Abreu, *Paracladius* Hirvenoja, and *Halocladius* Hirvenoja to be a strictly monophyletic group (LeSage & Harrison 1980). Four subgenera of *Cricotopus* are now recognised (Ashe 1983): *Cricotopus* s. str.; *Isocladius* Kieffer 1909; *Maurius* Lehmann 1971; and *Nostococcladius* Ashe & Murray 1980. All the known New Zealand species appear to belong to *Cricotopus* s. str. and this is true also of the known Australian fauna (Hergstrom 1974).

No review of the Austro-Pacific chironomid fauna is available but a catalogue is currently in preparation (Cranston, P.S., pers. comm.). Only one species has been described from Australia, *C. annuliventris* Skuse 1889 (Freeman 1961), but at least four new species are known to occur (Hergstrom 1974), although descriptions have yet to be published. Three species have been described from Micronesia (Tokunga 1964), all of which appear to differ from the known New Zealand species, although the type material has not been examined. Sublette & Sublette (1973) list 15 species from the Oriental region and several species are known from South Africa (Freeman 1956).

METHODS AND MORPHOLOGY

Counts and measurements were made on material collected from the Kaniwhaniwha Stream (37°54'S, 175°05'E), in the North Island, New Zealand, details of which are given by Boothroyd (1987). Larvae and imagines were prepared by heating for a few minutes in 5% KOH and passing through 70%–100% alcohol before mounting in euparal. Morphological nomenclature follows Sæther (1980). The term megaseta is used here in place of apical spine of the gonostylus (Sæther & Sublette 1983). Measurements are given as ranges, followed by a mean and the number (*n*) measurement in parentheses.

Generic diagnoses follow Sublette & Wirth (1980) for the imago, Coffman et al. (1986) for the pupa, and Cranston et al. (1983) for the larva.

All type material, together with pupal exuviae and larvae, has been deposited in the National Arthropod Collection, DSIR Plant Protection, Auckland, New Zealand.

SYSTEMATICS

Cricotopus van der Wulp, 1874

Type species. *Chironomus tibialis* Meigen 1818 by designation of Coquillett (1910).

Generic diagnosis

Imago. Eyes with a slight to moderate dorsal extension; with dense microtrichia. Temporal setae variable. Palpi normal. In some species pedicels with ventral setae in females. Antennae normally with 13 flagellomeres, occasionally reduced.

Anteprepronotum of moderate width to broad and collarlike, with the usual lateral clump of setae, occasionally with sparse setae near middle. Dorsocentral setae minute and decumbent ranging from uniserial to multiserial, occasionally broadly expanded so that the two rows join across scutum. Prealar setae usually restricted to a posterior group, occasionally expanded anteriorly into a row almost reaching parapsidal suture. Supra-alar and preepisternal setae present or absent. Acrostichals minute, decumbent, usually extending to near middle of scutum. Scutellar setae uniserial to multiserial.

Wing membrane glabrous. Venation of a modified *Orthocladus* type; C not extended to moderately extended past R4+5, which ends over or distal to apex of M3+4; CU1 at most moderately downcurved at tip. Squama partially to fully fringed.

Spurs similar to those of *Orthocladus*, rarely reduced to a single spur on middle and hind legs. Pulvilli present or absent. Small, curved, hyaline sensilla chaetica ("Sz sensilla" of Hirvenoja 1973) usually present on basal tarsomere of hind legs, present or absent on that of middle legs.

Abdominal chaetotaxy variable, ranging from a dense series covering most of middle terga to a variably reduced state; in some species there is a mid-dorsal, uniserial to biserial row of setae which may be darker and heavier than the remainder.

Ninth tergum variably setose; anal point usually absent, but if present, weakly to moderately developed; gonocoxite with 1 or 2 volsellae or without volsellae; endomeres present or absent; phallopodeme weakly chitinated; gonostylus with or without subapical flange, ranging from almost parallel sided to strongly bowed to apically inflated. Pupa. Small to medium sized pupae. Exuviae pale yellow or brown to dark brown.

Frontal setae present on frontal apotome or prefrons, or absent. Frontal apotome rugulose. Ocular field with 2 postorbital and no verticals. Thorax with 1–2 median and 0–2 lateral anteprepronotals. Thoracic horn variable in shape, usually tapering to point with spines on at least apical half, or blunt apically, elongate and with or without spines, sometimes small, globular and covered with rounded processes; horn sometimes blackish. Three precomae of variable length present; arrangement

dorsocentrals variable but usually in two pairs. ing sheath without pearls.

Abdominal shagreen pattern variable, often ridged into anterior and posterior fields on tergites VI in *C. (Cricotopus)*, but not divided into fields *C. (Isocladius)*; tergites VII–VIII often with weaker shagreen covering less area or sometimes without shagreen; tergite IX with anterior band of shagreen; sternites without shagreen or II–VIII with very weak shagreen. Tergite II usually with 2 regular rows of hooklets, sometimes with more than 2 rows interrupted medially. Pedes spurii A present on sternites IV–VI, sometimes also present on VIII but rarely weak; pedes spurii B usually present on segment rarely absent, sometimes also present on segment . Apophyses absent.

Abdominal setation: Segment I with 3–4 D, 1L and 1–2 V setae, II–VI with 3–5D, 3L and 3–4 V setae; VII with 3–5 D, 3–4 L and 3–4 V setae; VIII with 2 D, 4 L and 1V setae, sometimes 5 L setae appear present because of a lateral displacement of D setae. Anal lobe with 3 anal macrosetae, absent *C. (Nostococcladius)*; 2–3 median setae present in *(Nostococcladius)*, absent in other subgenera; fringe present; apex of lobe rounded, usually without spines, sometimes spines present; apex in lobe attenuated and sometime with coarse spines in *C. (Nostococcladius)*. Male genital sac shorter to longer than anal lobe.

larva. Medium sized larvae, up to 8 mm long.

Antenna with 5, occasionally 4, segments; segments consecutively shorter, or segments 3 and 4 subequal in length; occasionally antenna very short. Sensing organ on basal third of segment 1. Blade shorter than length of flagellum. Lauterborn organs usually distinct, sometimes vestigial or absent. Style shorter than length of segment 3.

Labrum SI usually bifid, rarely simple; remaining setae simple. Lateral lamellae absent. Chaetae simple or serrate; spinulae simple, weak. Pecten epipharyngis consisting of either 3 scales (in *Cricotopus* s. str. and *C. (Nostococcladius)*) or a single scale (in *C. isocladius*). Chaetulae laterales variable in number and shape; sometimes in *C. isocladius* first pair subequal in size to scale of pecten epipharyngis and could be mistaken for lateral scales of pecten epipharyngis; chaetulae basales with branched apices. Ungula generally U-shaped with short basal sclerite. Premandible with one or, rarely two, apical teeth; brush present or absent, when present, weak. Mandible apical tooth shorter than combined width of 3 inner teeth. Seta subdentalis apically pointed or notched with a hook. Seta interna

usually present and consisting of 6–7 simple or finely serrate branches, rarely absent. Outer margin usually crenulate, sometimes smooth, in *C. (Nostococcladius)* sometimes several flat, tooth-like projections present. Mola usually smooth, sometimes spines present. Mentum with one median and 6, rarely 5 or 7, pairs of lateral teeth present. Ventromental plate narrow; beard absent. Maxilla palpiger with triangular chaetulae. Lamellae of galea variable, usually dorsal pectinate lamellae present in *C. (Cricotopus)*; pecten galearis absent. Setae maxillaris simple.

Anterior parapods separate, each bearing an apical crown of claws; sometimes claw with a distinct apical tooth. Posterior parapods separate, each with an apical group of simple claws. Procerus about as high as wide, bearing 6–7 anal setae. Anal tubules variable in length, usually shorter than length of posterior parapods. Abdominal segments usually with 1 pair of setal tufts, sometimes only simple setae present.

Remarks. Imagines of *Cricotopus* are readily distinguished from all other Orthoclaudiinae, except for *Paracladius* and *Haloccladius*, by the following characters: eyes densely hairy, and short and fine dorsocentral setae. Most *Cricotopus* species can be separated from *Haloccladius* by the absence of anterior prealar setae (Sublette & Wirth 1980); if these setae are present then *Cricotopus* species have posteriorly converging dorsolateral setae and *Haloccladius* does not (Sublette & Wirth 1980). *Paracladius* species always have an anal point. Pupae of *Cricotopus* are often indistinguishable from those of *Orthoccladius*. However, the arrangement of the hooklets on Tergite II will often allow separation (Coffman et al. 1986). In the subgenera *Cricotopus* and *Isocladius* the hooklets are usually arranged in two rows, where those of *O. (Orthoccladius)* are usually in more than three rows. (Coffman et al. 1986). Larvae can be usually be distinguished from most other Orthoclaudiinae by the combination of a bifid SI and setal tufts on at least the first six abdominal segments (Cranston et al. 1983). Larvae with only simple setae on the abdomen cannot be readily separated from some *Orthoccladius*, except the *bicinctus* group, which has a serrated inner margin (mola) of mandible and the *trifascia* group (unique labial plate) (Simpson & Bode 1980).

Cricotopus vincenti n. sp.

Male imago ($n=8-9$, except where otherwise stated).

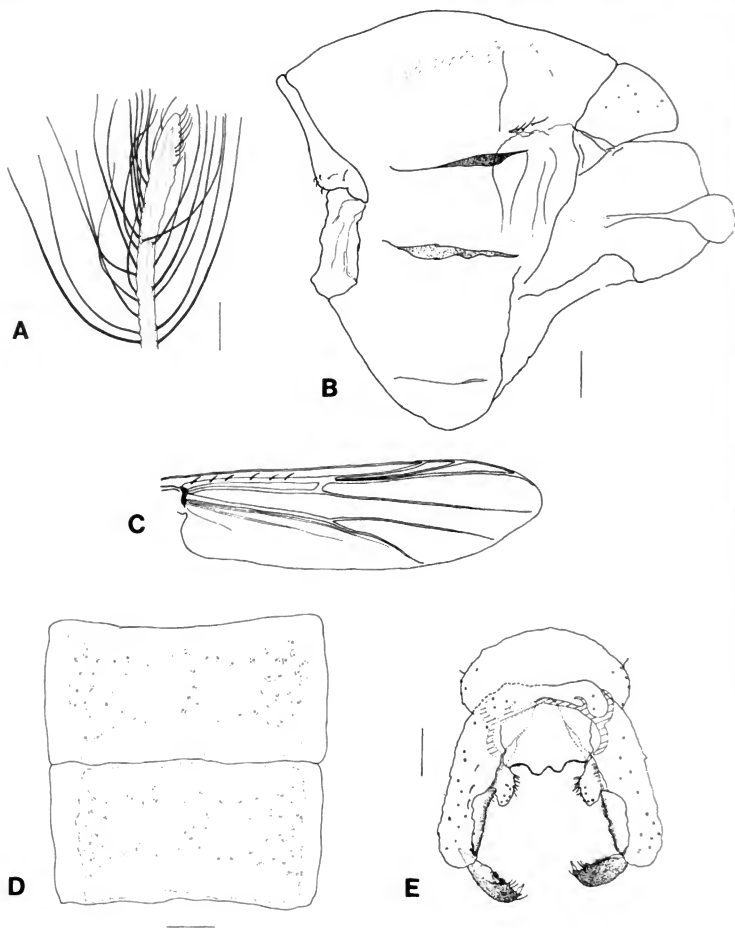


Fig. 1 Male Imago of *Cricotopus vincenti*. A, Apex of antenna; B, Thorax; C, Wing; D, Abdominal tergal chaetotaxy (segs. III and IV); E, Hypopygium. Scale bars: B, C, D = 0.1 mm; A, E = 0.05 mm.

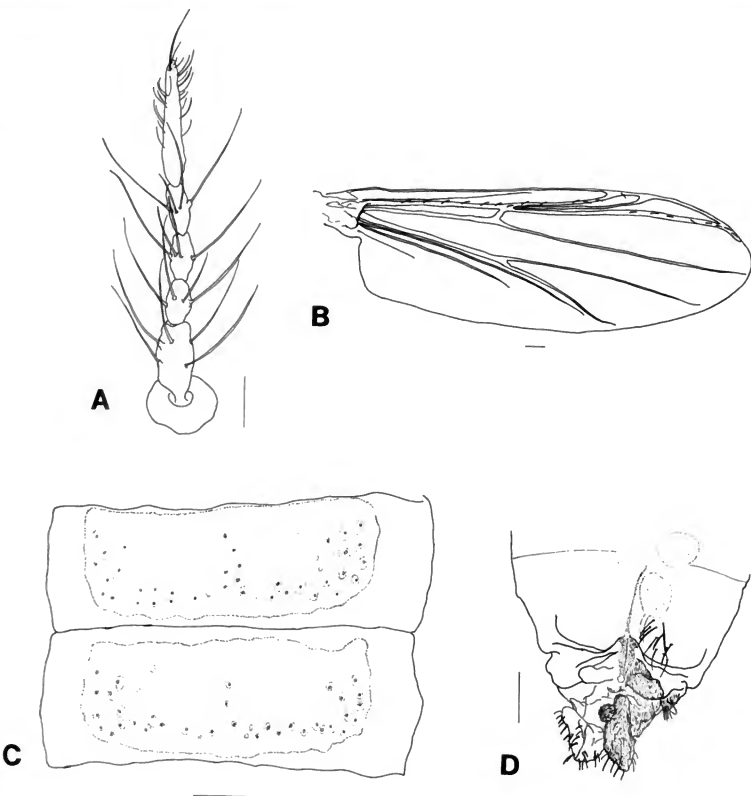


Fig. 2 Female Imago of *Cricotopus vincenti*. A, Antenna; B, Wing; C, Abdominal tergal chaetotaxy (segs. III and IV); D, Genitalia (ventral view). Scale bars: B, C, D, 0.1 mm; A, 0.05 mm.

Total length 2.94–3.94, 3.49 mm. Wing length 1.65–2.05, 1.94 mm. Total length/wing length 1.6–2.07, 1.81. Head dark, thorax and abdomen black; legs brown with no markings; hypopygium dark.

Antennal ratio 1.27–1.5, 1.34. Antenna with 13 flagellomeres; terminal flagellomere (Fig. 1A) length

480–570, 520 μ m. Temporal setae 9–11, including 4–5 outer verticals, 5–6 post orbitals. Palpal segment lengths (μ m): 40–50, 48 (4); 60–76, 63; 90–110, 96; 75–130, 110; 130–215, 179.

Anteprepronotum (Fig. 1B) laterally with 6–8 setae. Dorsocentrals 23–28, 25, in double row; prealars 4–6, 5 (4). Scutellum with 10 setae in double row.

Wing (Fig. 1C) V.R. 1.1–1.54, 1.19. Brachiolium no setae; R with 3–7, 5 setae; R_1 with 0–1 setae; other veins bare. Costa extended 65–88, 73 μ m (4). Squama with 13–17, 15 setae.

Spur of front tibia 45–55, 50 μ m (6) long; spurs of middle tibia 20–27.5, 24 μ m and 15–27.5, 22 μ m; spurs of hind tibia 40–80, 54 μ m and 25–40, 31 μ m. Width at apex of front tibia 27.5–40, 34 μ m; of middle tibia 35–45, 41 μ m; of hind tibia 37.5–55, 46 μ m. Comb of hind tibia with 12–13 setae, length range 17.5–47.5 μ m. Lengths (μ m) and proportions of legs:

	fe	ti	ta ₁	ta ₂
P ₁	620–750,680	750–875,836	570–620,587	280–320,298
P ₂	500–900,699	700–800,744	330–400,369	200–220,204
P ₃	650–720,691	750–925,838	440–560,495	240–270,249
	ta ₃	ta ₄	ta ₅	LR
P ₁	200–230,217	100–170,137	90–110,103	0.65–0.74,0.70
P ₂	130–170,153	100–120,107	100–110,101	0.47–0.53,0.50
P ₃	160–210,183	100–130,119	100–110,105	0.55–0.61,0.59
	BV	SV	BR	
P ₁	2.57–3.18,2.79	2.42–2.85,2.62	1.39–2.8,2.01	
P ₂	2.91–3.36,3.18	3.57–4.24,3.94	1.45–2.8,1.92	
P ₃	2.91–3.25,3.10	2.99–3.43,3.12	1.6–3.33,2.44	

Abdominal chaetotaxy of tergites III and IV is given in Fig. 1D. Hypopygium (Fig. 1E) Anal point absent. Gonocoxite length 200–240, 244 μ m (10) with posteriorly directed inferior volsella. Gonostylus 80–92.5, 88 μ m (10) long with megaseta 10–15, 14 μ m in length. HR 2.29–2.74, 2.55 (10); HV 1.83–2.24, 2.06 (8).

Female imago ($n = 7-8$, except where otherwise stated)

Total length 2.5–3.13, 2.76 mm. Wing length 1.95–2.25, 2.14 mm. Total length/wing length 1.11–1.54, 1.31. Colour similar to male but thoracic shoulders paler.

Antennal ratio 0.48–0.82, 0.59. Flagellomere lengths (μ m): 27.5–85.0, 66; 35–52.5, 44; 37.5–52.5, 48; 32.5–52.5, 47; 105–128, 121 (Fig. 2A). Palp lengths (μ m): 45–60, 54; 65–135, 98; 80–195, 121; 110–250, 168; 165–245, 203.

Anteprepronotum laterally with 5–7, 6 setae. Dorsocentrals 21–28, 25 (5) in double row, acrostichals 7–13, 10 (3); prealars 4. Scutellum with 12–16, 14 (5) setae.

Wing (Fig. 2B) VR 1.11–1.67, 1.26 (6). Brachiolium 0–1 setae, R with 8–11, 8 (6) setae, R_1 with 4–6, 5 (5), R_{4+5} with 6–12, 8 (5) setae. Costa extended 75–250, 156 m (4). Squama with 10–16, 14 (5) setae.

Legs. Spur of front tibia 27.5–55, 40 μ m long; spurs of middle tibia 22.5–42.5, 28 μ m and 17.5–22.5, 20 μ m long; spurs of hind tibia 47.5–65, 55 μ m and 22.5–40, 31 μ m long. Width at apex of front tibia 37.5–52.5, 43.8 μ m; of middle tibia 40–52.5, 45.3 μ m; of hind tibia 45–55, 51.3 μ m. Comb of hind tibia with 11–16, 13 setae, length range 20–47.5 μ m. Lengths (μ m) and proportions of legs:

	fe	ti	ta ₁	ta ₂
P ₁	600–820,690	725–900,824	530–700,580	270–240,301
P ₂	600–775,699	675–775,741	300–400,345	120–210,196
P ₃	550–720,668	750–900,825	430–510,478	220–270,249
	ta ₃	ta ₄	ta ₅	LR
P ₁	190–270,266	110–190,155	100–120,105	0.59–0.93,0.71
P ₂	140–170,155	90–110,101	90–110,99	0.40–0.52,0.47
P ₃	150–200,185	110–120,111	100–110,103	0.53–0.61,0.58
	BV	SV	BR	
P ₁	2.52–3.05,2.68	2.00–3.08,2.64	1.42–2.25,1.89	
P ₂	3.06–3.42,3.24	3.88–4.46,4.19	1.27–1.82,1.54	
P ₃	2.86–3.30,3.05	2.96–3.37,3.13	1.64–2.17,1.90	

Abdominal chaetotaxy of tergites III and IV is given in Fig. 2C.

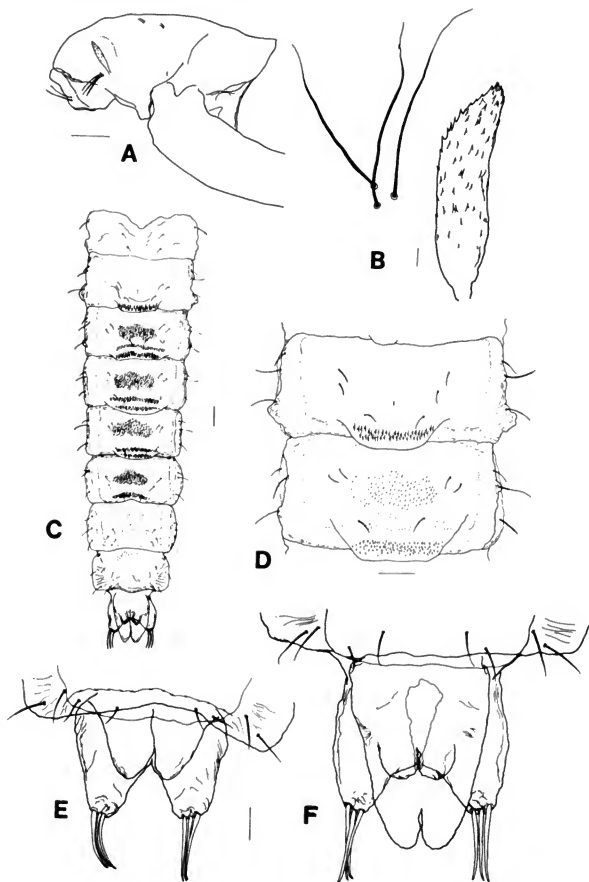
Gonocoxite (Fig. 2D) of female with 6–11, 7 setae. Gonopophysis with 8–9 (2) setae. Cercus 130–160, 140 μ m long. Seminal capsule 72.5–92.5, 81 μ m long and 55–80, 68 μ m wide.

Pupa ($n = 13-15$, except where otherwise stated).

Total length 3.12–3.72, 3.4 mm. Exuvia pale and transparent.

Cephalothorax. Frontal setae absent. Thorax as in Fig. 3A. Median anteprepronotals 2, 100–135, 117 μ m (9) long; lateral anteprepronotals absent. Anterior precorneal seta 62.5–143, 118.6 μ m long, median 70–133, 115 μ m long, posterior 80–140, 123 μ m long. Distance between anterior and posterior seta 10–17.5, 15 μ m. Thoracic horn (Fig. 3B) 125–163, 140 μ m long, 23–35, 29 μ m wide. Dorsocentrals robust; Dc₁ 45–70, 58 μ m (11) long; Dc₂ 45–95, 73 μ m (11) long; Dc₃ 43–80, 59 μ m (10) long; Dc₄ 50–75, 58 μ m (11) long. Distance between Dc₁ and Dc₂ 17.5–30, 25 μ m (11); between Dc₂–Dc₃ 115–230, 156 μ m (11); between Dc₃ and Dc₄ 13–28, 23 μ m

Fig. 3 Pupa of *Cricotopus vincenti*. A, Thorax; B, Thoracic horn and precorneal setae; C, Abdomen (dorsal view); D, Abdominal tergal chaetotaxy, tergites II and III; E, Anal lobe (♀); F, Anal lobe (♂). Scale bars: A, C = 0.1 mm; D, E, F = 0.05 mm; B = 0.01 mm.



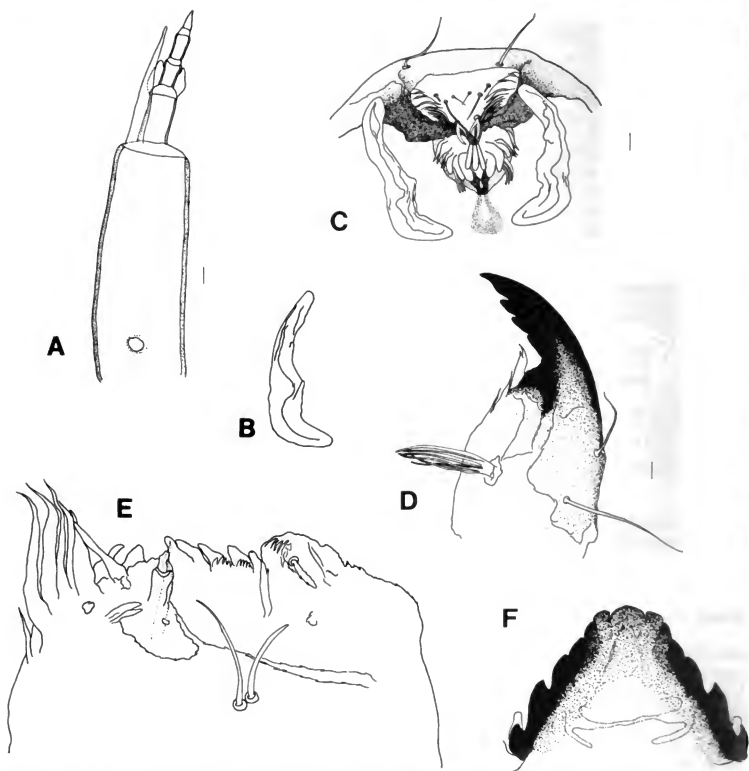


Fig. 4 Larva of *Cricotopus vincenti*. A, Antenna; B, Premandible; C, Labrum and epipharynx; D, Mandible; E, Maxilla; F, Mentum; Scale bars: A-F = 0.01 mm.

(11). Single prealar seta. Wing margin, 1.08–1.2, 1.14 mm (11) long, 0.33–0.44, 0.6 mm (11) wide.

Abdominal shagreen and chaetotaxy as in Fig. 3C, and of Tergites II and III in Fig. 3D. Caudal projection on TII 175–325, 258 μ m (11) wide, with 46–60, 50(9) hooklets, length range 12.5–37.5 μ m. Anal lobe (Fig. 3E and 3F) 160–265, 214 μ m long. Outer

apical macroseta 105–137.5, 117.1 μ m long; median 95–127.5, 108.8 μ m; inner 97.5–120, 110.4 μ m long.

Larva ($n = 24$ –25 except when otherwise stated)

Body length 3.13–4.81, 4.04 mm (35); head capsule length 450–525, 479 μ m (38), head capsule width 300–475, 346 μ m (38). Body colour green; after

reservation pale yellow. Head capsule pale yellow with a dark postoccipital margin.

Antenna 5-segmented (Fig. 4A). Lengths (μm) 43.8–75, 52.2; 12.5–16.3, 13.6; 5.0–6.3, 5.05; 5.0–6.3, 8.9, 2.5–6.3, 4.01. AR, 1.56–2.0, 1.82 (19). Basal antennal segment 18.8–27.5, 22.4 μm wide; distance from base to ring organ 7.5–12.5, 9.86 μm (18); antennal blade 17.5–27.5, 23.75 μm (4) long. Remandible 77.5–102.5, 90 μm (22) long (Fig. 4B). Labrum and epipharyngeal area is in Fig. 4C. Mandible (Fig. 4D); length of apical tooth 15–22.5, 19.4 μm long, combined length of inner teeth 40–50, 33.4 μm . Mola with spines and seta interna of 6–7 branches. Maxilla as in Fig. 4E. Mentum (Fig. 4F) with single median tooth 17.5–22.5, 20.0 μm wide and 6 pairs of lateral teeth. Flattened mentum width 138–188, 157.39 μm (26).

Abdomen. Posterior parapods 150–230, 186.2 μm (17) long, 85–140, 120.6 μm (17) wide. Procercus 20–32.5, 24.7 μm long, bearing 4–5 anal setae, maximum length 380–450, 410 μm (15). Supra-anal seta 65–80, 73.8 μm (8) long. Anal tubules 100–125, 117.5 μm (10) long, 55–90, 66.4 μm (10) wide.

Etymology. Named after the author's late father, Kenneth Vincent Boothroyd.

Material examined. Holotype male collected from light trap, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 16 January 1985, leg. I.K.G. Boothroyd, in coll. New Zealand Arthropod Collection, Department of Scientific and Industrial Research, Auckland, New Zealand. Allotype female reared from larva with pupal exuviae and cast larval skin, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 20 January 1986. Paratypes, five males reared from larvae, with pupal exuviae and cast larval skins, 4 males collected from light trap, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 1985–86. Five females reared from larvae, with pupal exuviae and cast larval skins, 2 collected from light trap, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 1985–1986. Allotype, 5 males, 4 females, 8 pupal exuviae and 15 larvae deposited in the New Zealand Arthropod Collection, Department of Scientific and Industrial Research, Auckland, New Zealand, remainder in the collection of I.K.G. Boothroyd, Waikato Regional Council, Hamilton, New Zealand.

Remarks. *C. vincenti* is similar to *C. aucklandensis* from the Auckland Islands but the adult male differs in having a much higher antennal ratio, more anteprenotal setae, and a more distinct flange on the gonostylus. The pupa of *C. vincenti* can be separated from *C. aucklandensis* by the thoracic horn (clubbed in *C. aucklandensis*), presence of shagreen on abdominal tergites VII and VIII, and the lack of distinctive muscle marks. Larvae of the two species are readily distinguished by the large median tooth of the mentum in *C. aucklandensis*, and the trifasciate mentum of *C. vincenti*. *C. vincenti* is readily distinguishable from the remaining known New Zealand *Cricotopus* species as there are no tibial or abdominal markings. It is similar also to the South African *C. obscurus* Freeman, but I have examined the holotype of *C. obscurus* in the British Museum (Natural History) and *C. vincenti* differs in being larger, having a higher A.R., a distinct abdominal chaetotaxy, and by having a larger posteriorly directed inferior volsella and a definite flange on the gonostylus.

The presence of the thoracic horn of the pupa of *C. vincenti* will separate it from pupae of *C. planus*. Pupae of *C. vincenti* and *Paratrachocladus pluriserialis* Santos Abreu are similar, but the thoracic horn of *C. vincenti* is larger and the abdominal shagreen is not separated into isolated patches on the tergites. Larvae of *C. vincenti* are readily distinguishable from *C. planus* by the absence of a distinct notch on the outer margin of the mandible, and the trifasciate mentum characteristics. Larvae can also be distinguished from *P. pluriserialis* by the presence of spines along the inner margin of the mandible.

Ecology. Larvae of *C. vincenti* have been shown (as *Cricotopus* Indent. Sp. B) to be abundant in the summer months and rare or absent during the winter (Boothroyd 1987). Similarly, emergence of imagines occurred continuously throughout the summer in the Kaniwhaniwha Stream but pupal exuviae were found at other times of the year (Boothroyd 1988) and the number of generations was unclear.

Cricotopus planus n. sp.

Male imago ($n = 12$ –15, except when otherwise stated).

Total length 3.0–3.75 3.43 mm. Wing length 1.75–2.38, 2.12 mm. Total length/wing length 1.33–1.93,

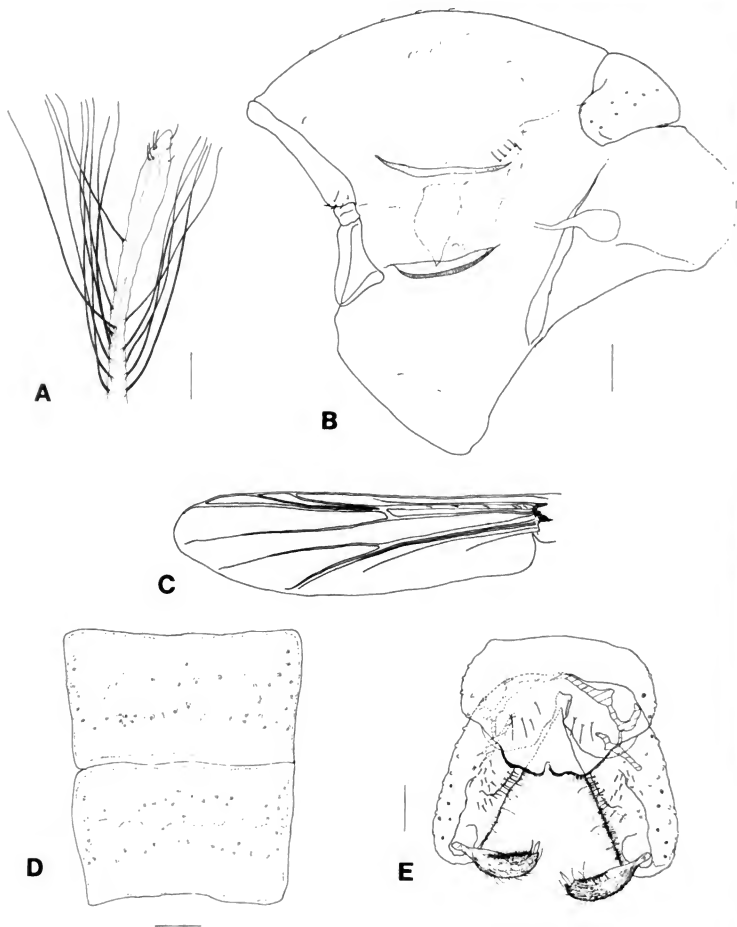


Fig. 5 Male Imago of *Cricotopus planus*. A, Apex of antenna; B, Thorax; C, Wing; D, Abdominal tergal chaetotaxy (segs. III and IV); E, Hypopygium. Scale bars: B, C, D = 0.1 mm; A, E = 0.05 mm.

.62. Head dark, thorax black stripes on dark brown background. Legs brown with no markings. Abdomen black with yellow markings on basal third of segment 2 and basal halves of segments 4 and 5. Hypopygium paler.

Antennal ratio 1.02–1.24, 1.05. Antenna with 13 flagellomeres; terminal flagellomere (Fig. 5A) length 20–480, 446 μ m. Temporal setae 6–9, including 3–4 outer verticals, 3–4 orbitals. Palpal segment lengths (μ m): 60–120, 84 (6); 45–100, 67.5 (10); 100–135, 17 (10); 110–135, 123 (10); 195–240, 216 (10).

Antepnotum (Fig. 5B) with 3–5, 4 lateral setae. Dorsocentrals 23–30, 26 (10) setae in triple row, acrostichals 6–9, 7 (6); prealars 4–5, 4. Scutellum with 12–18, 14 setae.

Wing (Fig. 5C) VR 1.07–1.2, 1.2. Brachiolium with 1 seta; R with 4–9, 5 setae; other veins bare. Costa extended 55–75, 67 μ m (9). Squama with 8–18, 12 setae.

Spur of front tibia 20–50, 40 μ m long; spurs of middle tibia 22.5–35, 28 μ m (9) and 17.5–35, 26 (9); spurs of hind tibia 40–62.5, 55 μ m and 22.5–32.5, 27 μ m. Width at apex of front tibia 35–55, 44 μ m; of middle tibia 40–52.5, 45 μ m; of hind tibia 42.5–55, 50 μ m. Comb of hind tibia with 10–12 setae, length range 22.5–55 μ m. Lengths (μ m) and proportions of legs:

	fe	ti	la ₁	la ₂
P ₁	700–875, 788	750–1100, 963	490–730, 638	240–420, 329
P ₂	650–912, 792	710–925, 818	310–650, 423	160–380, 228
P ₃	580–875, 761	580–1025, 907	360–600, 520	190–410, 278
	la ₃	la ₄	la ₅	LR
P ₁	150–270, 238	140–190, 158	90–120, 108	0.51–0.73, 0.67
P ₂	130–200, 170	90–170, 114	90–120, 100	0.37–0.87, 0.52
P ₃	150–240, 217	110–140, 127	90–110, 103	0.49–0.61, 0.57
	BV	SV	BR	
P ₁	2.38–3.38, 2.89	2.53–3.53, 2.77	1.36–2.20, 1.72 (9)	
P ₂	2.59–3.68, 3.37	2.35–3.40, 3.94	1.39–2.33, 1.72 (11)	
P ₃	2.06–3.64, 3.07	2.96–3.64, 3.23	1.60–2.70, 2.15 (9)	

Chaetotaxy of abdominal tergites III and IV is shown in Fig. 5D.

Hypopygium (Fig. 5E). Anal point absent. Gonocoxite length 210–250, 234 μ m, with a low and flattened inferior volsella. Gonostylus 77.5–105, 90 μ m long with megaseta 15–22.5, 18.9 μ m in length. HR 2.38–2.84, 2.61; HV 1.42–2.21, 1.82.

Female imago ($n = 8–11$, except when otherwise stated).

Total length 2.19–2.69, 2.47 mm. Wing length 1.8–2.23, 2.04 mm. Total length/wing length 1.19–1.33, 1.21 mm. Colour similar to male.

Antennal ratio 0.36–0.57, 0.47 (Fig. 6A). Flagellomere lengths (μ m): 45–85, 70; 40–50, 44; 40–50, 45; 40–50, 44; 80–107.5, 96. Temporal setae 1–7 including 3–5, 4 outer verticals and 1–2 orbitals. Palp lengths (μ m): 50–85, 66 (4); 50–60, 55 (4); 90–125, 106 (6); 110–135, 120 (6); 215–240, 221 (6).

Antepnotum with 3–5 lateral setae. Dorsocentrals 25–30, 28 (3) setae, in triple row, acrostichals 5–10, 8 (3), prealars 4–5, 4 (8). Scutellum with 22–32, 26 (8) setae.

Wing (Fig. 6B) VR 1.07–1.19, 1.13 (8). Brachiolium with 1 seta (7), R with 5–9, 7 (7) setae, R₁ with zero, R₄₊₅ with 0–9, 3 (7) setae. Costa extended 62.5–87.5, 75 μ m (6). Squama with 8–14, 11 (8) setae.

Spur of front tibia 35–42.5, 38 μ m long; spurs of middle tibia 22.5–35, 28 μ m and 20–30, 25 μ m; spurs of hind tibia 50–60, 55 μ m and 22.5–40, 29 μ m. Width at apex of front tibia 30–47.5, 40.5 μ m; of middle tibia 35–50, 43 μ m; of hind tibia 45–58, 52 μ m. Comb of hind tibia with 10–12, 11 setae, length range 22.5–50 μ m. Lengths (μ m) and proportions of legs:

	fe	ti	la ₁	la ₂
P ₁	700–825, 753	750–1000, 844	390–590, 526	260–310, 281
P ₂	675–800, 731	725–825, 764	300–420, 376	180–220, 199
P ₃	700–850, 736	725–950, 836	470–570, 503	200–290, 241
	la ₃	la ₄	la ₅	LR
P ₁	150–240, 210	100–160, 140	90–100, 97	0.52–0.72, 0.62
P ₂	150–190, 157	90–110, 99	90–100, 92	0.41–0.52, 0.49
P ₃	150–230, 193	90–120, 109	90–110, 99	0.57–0.68, 0.60
	BV	SV	BR	
P ₁	2.56–3.50, 2.94	2.63–3.85, 3.08	1.46–2.14, 1.84	
P ₂	3.10–3.71, 3.41	3.68–4.83, 4.04	1.17–1.78, 1.53	
P ₃	2.99–3.89, 3.25	2.91–3.73, 3.12	1.42–2.00, 1.61	

Chaetotaxy of abdominal tergites III and IV are shown in Fig. 6C.

Gonocoxite (Fig 6D) with 5–7, 6 setae. Cercus 110–160, 141 μ m long. Seminal capsule 60–75, 68 μ m long, 40–60, 54 μ m wide.

Pupa ($n = 20–25$, except when otherwise stated).

Total length 3.13–4.38, 3.78 mm. Exuviae golden brown.

Cephalothorax. Frontal setae absent. Thorax as in Fig. 7A. Median antepnotals 100–140, 112 μ m

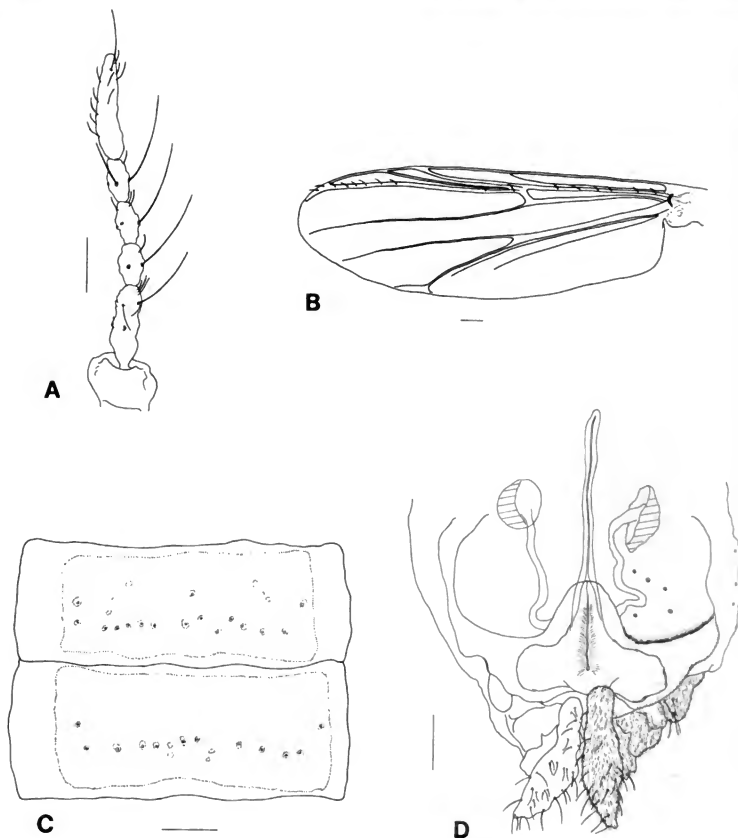
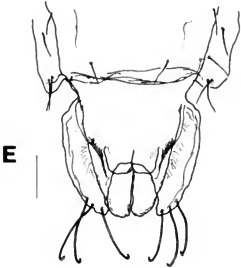
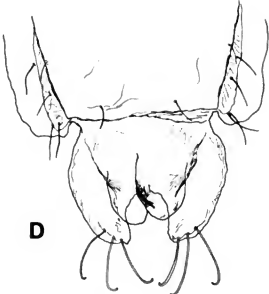
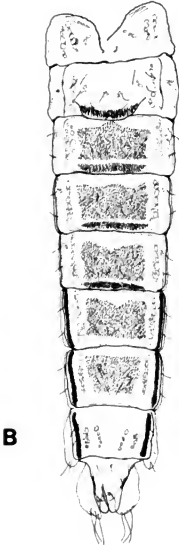
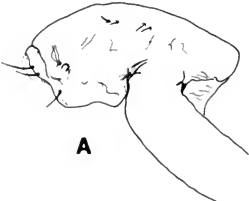


Fig. 6 Female Imago of *Cricotopus planus*. A, Antenna; B, Wing; C, Abdominal tergal chaetotaxy (segs. III and IV); D, Genitalia (ventral view). Scale bars: B, C = 0.1 mm; A, D = 0.05 mm.

Fig. 7 Pupa of *Cricotopus planus*. A, Thorax; B, Abdomen (dorsal view); C, Abdominal tergal chaetotaxy, tergites II and III; D, Anal lobe (♀); E, Anal lobe (♂). Scale bars: A, C, D, E, F = 0.1 mm; B = 0.01 mm.



(17) and 50–100, 75 μ m (13) long; lateral anteprenotal 57.5–95, 75 μ m (13) long. Anterior precorneal seta 105–142.5, 121 μ m long; median 100–142.5, 120 μ m; posterior 112.5–142.5, 126 μ m long. Distance between anterior and posterior 12.5–22.5, 16.1 μ m (16). Thoracic horn absent. Dorsocentrals robust; Dc₁ 42.5–67.5, 53 μ m long; Dc₂ 45–75, 55.6 μ m; Dc₃ 22.5–62.5, 36.8 μ m; Dc₄ 20–55, 41.4 μ m. Distance between Dc₁ and Dc₂ 25–57.5, 39.4 μ m (18); between Dc₂ and Dc₃ 145–225, 185 μ m (19); Dc₃ and Dc₄ 25–55, 33.7 μ m (19). Wing margin 1.13–1.58, 1.35 mm long, 0.33–0.5, 0.42 mm wide.

Abdominal shagreen and chaetotaxy is shown in Fig. 7B and of tergites II and III in Fig. 7C. Peres spurii absent. Caudal projection on TII 320–650, 412 μ m (15) wide, with 48–74, 60 (14) hooklets, length range 7.5–55.0 μ m. Anal lobe (Fig. 7D, E) 250–330, 299 μ m long. Outer apical macroseta 125–195, 163 μ m long; median 120–185, 155 μ m; inner 125–170, 145 μ m.

Larva ($n = 22$ –26, except when otherwise stated)

Body length 2.63–4.94, 3.77 mm; head capsule length 0.4–0.475, 0.433 mm; head capsule width 0.275–0.325, 0.30 mm. Body colour green; yellow/green after preservation, head capsule dark brown, darker at posterior edge.

Head. Antenna 5-segmented (Fig. 8A). Lengths (μ m) 37.5–47.5, 45.2; 10–12.5, 11.4; 2.5–3.75, 3.3; 3.75–5.0, 4.8; 2.5–5.0, 3.0. AR 1.71–2.53, 2.01. Basal antennal segment 17.5–22.5, 20 μ m wide; distance from base to ring organ 7.5–10.0, 9.5 μ m (16). Premandible 77.5–92.5, 83.0 μ m (19) long. Labrum and epipharyngeal area as in Fig. 8B. Length of mandible (Fig. 8C) apical tooth 15–22.5, 17.9 μ m; combined length of inner teeth 25–29, 27 μ m. Mola with 2–3 spines and seta interna with 6–8 branches. Outer margin crenulated, with distinctive notch. Maxilla as in Fig. 8D. Mentum (Fig. 8E) with single median tooth 15–25, 19 μ m wide and 6 pairs of lateral teeth. Flattened mentum width 105–125, 114 μ m.

Abdomen. Posterior parapods 125–230, 189 μ m long, 110–185, 143 μ m long. Procerus 20–25, 23 μ m long, bearing 5–7 anal setae, maximum length 350–490, 409 μ m (13). Anal tubules 150–205, 180 μ m (12) long, 50–100, 72 μ m (12) wide.

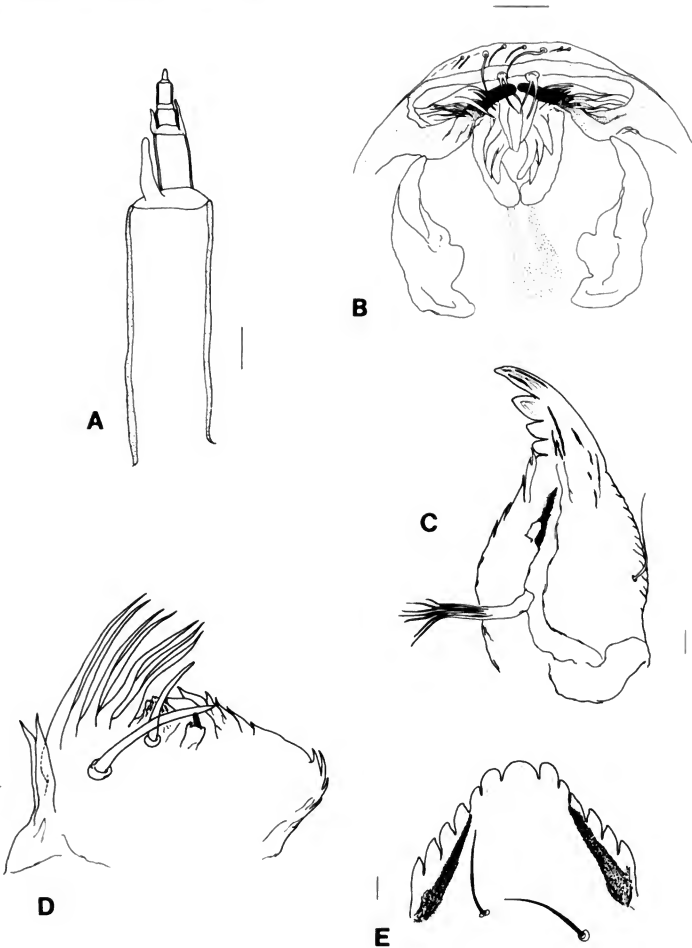
Etymology. From the Latin "planus" (even, flat) alluding to the flattened inferior volsella.

Material examined. **Holotype** male caught over stream, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 14 October 1984, leg. I.K.G. Boothroyd, deposited in the New Zealand Arthropod Collection, Department of Scientific and Industrial Research, Auckland, New Zealand. **Allotype** female collected in light trap, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 14 October 1984. **Paratypes**, five males reared from larvae with pupal exuviae and cast larval skins, 3 collected from light traps, 6 caught over stream; 5 females reared from larvae with pupal exuviae and cast larval skins, 5 collected from light traps; 15 pupal exuviae and 16 larvae collected from stream, Kaniwhaniwha stream, 37°54'S, 175°05'E, 60 m asl, Mt Pirongia, North Island, New Zealand, 1984–1985. **Allotype**, 8 males, 6 females, 10 pupal exuviae and 12 larvae deposited in the New Zealand Arthropod Collection, Department of Scientific and Industrial Research, Auckland, New Zealand, remainder in the collection of I.K.G. Boothroyd, Waikato Regional Council, Hamilton, New Zealand.

Remarks. *C. planus* has similar abdominal markings to *C. cingulatus* but differs from the holotype in hypogial structure, *C. planus* having a small, low and flattened inferior volsella whereas *C. cingulatus* has a clearly pronounced posteriorly-directed inferior volsella. Gonostylus similar, but *C. planus* has a more pronounced triangular point near megaseta. *C. planus* can be distinguished from the remaining known New Zealand *Cricotopus* species by a combination of the presence of abdominal markings and the absence of white rings on the tibia.

Larvae are readily distinguishable from *C. vincens* and *C. aucklandensis* by mentum and mandible morphology. The mandible is clearly distinguishable with a crenulated outer margin and a distinctive "notch" opposite the seta subdentalis. The pupa can be distinguished from other known *Cricotopus* species by its abdominal shagreen patterns, and lack of thoracic horn.

Ecology. Larvae of *C. planus* were found in the riff areas of a fast flowing stream but were rarely found in pools. They formed tubes from algae and detritus. Larvae were present at all times of the year.



g. 8 Larva of *Cricotopus planus*. A, Antenna; B, Labrum and epipharynx; C, Mandible; D, Maxilla; E, Mentum; ale bars: A–E = 0.01 mm.

(Boothroyd 1987—as *C. cingulatus*) but densities fluctuated and no real pattern was evident. Emergence of adults was commonest in spring (Boothroyd 1988—as *Cricotopus* Indet. Sp.X), but occurred throughout the year. Swarms of adult males were observed in the early evenings of spring, along the banks of the river.

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Reassessment of *Ctenopseustis* Meyrick and *Planotortrix* Dugdale with descriptions of two new genera (Lepidoptera: Tortricidae)

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Abstract Current pheromonal, behavioural, and adult morphological studies force a reassessment of the genera *Ctenopseustis* Meyrick and *Planotortrix* Dugdale, which include endemic primary orchard leafroller horticultural pests. *Ctenopseustis* includes five species: *obliquana* (Walker) restricted (with *purcatana* (Walker) *transtrigana* (Walker), *turbulentana* (Walker), *ropeana* (Felder & Rogenhofer), *characterana* (Meyrick) as synonyms); *herana* (Felder & Rogenhofer), [with *inana* (Butler) as synonym]; *servana* (Walker) (synonymy as in Green & Dugdale 1982); *fraternana* Philpott; and *filicis* new species. The existence of a North Island entity morphologically similar but pheromonally distinct from sympatric *obliquana*, and morphologically distinct but pheromonally indistinguishable from allopatric *herana* is reported. *Planotortrix* is restricted to *excessana* (Walker) [with synonym *biguttana* (Walker)], *octo* new species, *octoides* new species, *vicenniana* new species, *puffini* new species, *flammea* (Salmon), and *notophaea* (Turner).

Two new genera are described: *Apoctena*, new genus for *conditana* Walker, *n. comb.*, type species; *flavescens* Butler *n. comb.*; *clarkei* Philpott *n. comb.*; *orthocopa* Meyrick *n. comb.*; *orthopsis* Meyrick *n. comb.*; *persecta* Meyrick *n. comb.*; *spatiosa* Philpott *n. comb.*; *syntona* Meyrick *n. comb.*; *tigris* Philpott *n. comb.*; and *Leucotenes* new genus, for the species *coprosmae* Dugdale (with *Tortrix characterana* auct., nec Meyrick, 1881, as synonym) *n. comb.*

Keywords Lepidoptera; Tortricidae; Archipini; *Ctenopseustis*; *Planotortrix*; *Apoctena* n.g.; *Leucotenes* n.g.; pheromones; systematics

INTRODUCTION

Archipini in New Zealand (and Australia) are divisible into two distinct groups differing in male genital valval structure (Dugdale 1966b, 1971; Horak 1984). One group has the valva more or less triangular and lacking a costa, with the inner face "plicate" (Horak 1984), whereas the other group has the valva more or less oblong and with a strong costa, with the inner face not plicate or folded (a "simple" valva, Horak 1984). In New Zealand, the first group – the "true Archipini" – is represented by less than 20 species in 5 genera, including the adventive *Epiphyas postvittana* (Walker) from Tasmania and south-east Australia. The second group is dominant (Dugdale 1966b, 1988) and includes the 4 genera discussed in this paper, as well as 17 other genera, including *Catantaria* Meyrick, *Ecclitica* Meyrick, *Epichorista* auct., *Gelophaula* Meyrick, *Harmologa* Meyrick, and *Pyrgotis* Meyrick, and over 130 species.

Before 1984, the New Zealand orchard-infesting *Ctenopseustis* species or brown-headed leafroller (BHLR), and *Planotortrix* species or green-headed leafroller (GHLR) (both Lepidoptera: Tortricidae) were thought to be two species only, *Ctenopseustis obliquana* (Walker) sensu Green & Dugdale 1984, and *Planotortrix excessana* (Walker), sensu Dugdale 1966a. These endemic leafrollers were classed as primary orchard pests (Wearing et al. 1990 in press) affecting horticultural and, to a lesser extent, silvicultural management in New Zealand.

Intensive studies on the female-produced sex pheromones of these species from many localities, since 1984 (Galbreath et al. 1985; Young et al. 1985; Foster et al. 1986; Foster & Dugdale 1988; Foster et al. 1989) have shown that the entities BHLR and GHLR each include sibling or cryptic species. The studies were extended whenever opportunity arose to include other species morphologically classed as either *Planotortrix* or *Ctenopseustis*, and to include populations from the Chatham Islands, some 800 km east of the South Island. Isozyme analyses and morphological comparisons gave results congruent with the pheromone results (C. White, pers. comm.).

Besides the economic importance of the BHLR and GHLR species complexes, the two genera are of interest: (1) because their sex pheromones are unusual in Tortricinae, being probably derived via $\Delta 9$ or $\Delta 10$ desaturation (as summarised by Foster & Dugdale 1988), rather than via $\Delta 11$ desaturation as found in the majority of Tortricinae examined to date (Roelofs & Brown 1982; Arn et al. 1986); (2) their morphologies are "rich in plesiomorphies" (Horak 1984: 20); and (3) as became evident in the course of the studies since 1983, we were accumulating behavioural, biochemical, and morphological data on what appears to be the complete extant range of two presumed monophyletic groups (i.e., groups morphologically definable on postulated synapomorphies). Such studies based on monophyletic groups of species rather than on single species from diverse groups may be more useful for comparative evolutionary studies.

The purpose of this paper is to formalise nomenclature, assign synonyms, and give taxonomic diagnoses of the entities now recognised as a result of the studies carried out by members of Entomology Division, DSIR (now DSIR Plant Protection) on the *Ctenopseustis* and *Planotortrix* complex since 1983.

The genera *Ctenopseustis* and *Planotortrix* are here redefined, and two new genera are proposed: *Apoctena* nov., and *Leucotenes* nov. The four genera together form a distinctive morphological and colour pattern set within the New Zealand tribe Archipini (sensu Horak 1984: 8–9), subfamily Tortricinae.

The necessity to define the use of the term "species" in a study (as stressed by Mishler & Donoghue 1982; Ackery & Vane-Wright 1984) is recognised here. The characters used for elucidating and describing the species recognised in this study are in two groups:

- (a) A communication system that allows sexual communication between the members of a population and which is not recognised in full by members of other populations.
- (b) Unique patterns of morphological or genetic markers and frequencies of genetic characters.

In Tortricidae, the female-produced sex pheromone elicits relatively long-distance activation of the male; in response, the male flies upwind to the

pheromone source, i.e., the female (Roelofs & Carde 1974). In this way the two sexes are brought together and copulation generally results. Characterisation of the sex pheromone can therefore be a valuable aid in the differentiation and classification of species where no morphological differences are discernible in structures used in mating behaviour (see, for example Roelofs & Carde 1974: 97).

States of the first group of characters form an important determinant of mating fidelity between members of a presumed species, and would exclude interspecific matings in the wild. For the second group, the states are the results of such fidelity. Morphological characters were found to be consistent in laboratory-reared pure lines, in specimens collected in sticky traps baited with relevant compounds, and in field-collected specimens accumulated over the last 136 years.

In the following descriptions, the area code of Crosby et al. (1976), e.g., Moutere Hills (NN) is used here. Sex pheromone components acronyms are as follows: Z5–14:OAc for (Z)–5–tetradecenyl acetate; Z7–14:OAc for (Z)–7–tetradecenyl acetate; Z8–14:OAc for (Z)–8–tetradecenyl acetate; Z10–16:OAc for (Z)–10–hexadecenyl acetate; and Z11–14–OAc for (Z)–11–tetradecenyl acetate.

The study is based on approximately 3900 specimens in NZAC.

DESCRIPTIONS

The *Ctenopseustis* – *Planotortrix* subgroup of genera.

This subgroup is distinguishable from most other members of the "oblong-valva" group in Archipini by the following character states in combination:

- (1) labial palpi porrect and beak-like, sometimes very long (range: 2.0–4.0× horizontal diameter of the compound eye). There are two exceptions: *Apoctena orthopsis* Meyrick, and *A. pictoriana* F & R.
- (2) thorax and tegulae smooth-scaled (i.e., not crested, nor with erect scales)

Fig. 1–8 (this and following 3 pages) Distribution maps (solid symbol – records based on female sex pheromone analysis and/or capture of males in sex pheromone baited sticky traps; hollow symbol record based on adult morphology only); 1 *Ctenopseustis obliquana* (Walker) Note: North Island morphological records may include *Ct.* "Type II North I."; 2 *Ct. herana* (Felder & Rogenhofer), South Island; and *Ct.* "Type II North I.", North Island based on pheromone analyses, (solid symbols), and male trapping (T); 3 *Ct. fraterna* Philpott, North Island; *Ct. filicis* n. sp., South and Stewart Islands; 4 *Ct. servana* (Walker); 5 *Planotortrix excessana* (Walker); 6 *P. octo* n. sp.; 7 *P. avicenniae* n. sp., North Island; *P. puffini* n. sp., South and Stewart Islands; 8 *P. flammea* (Salmon).

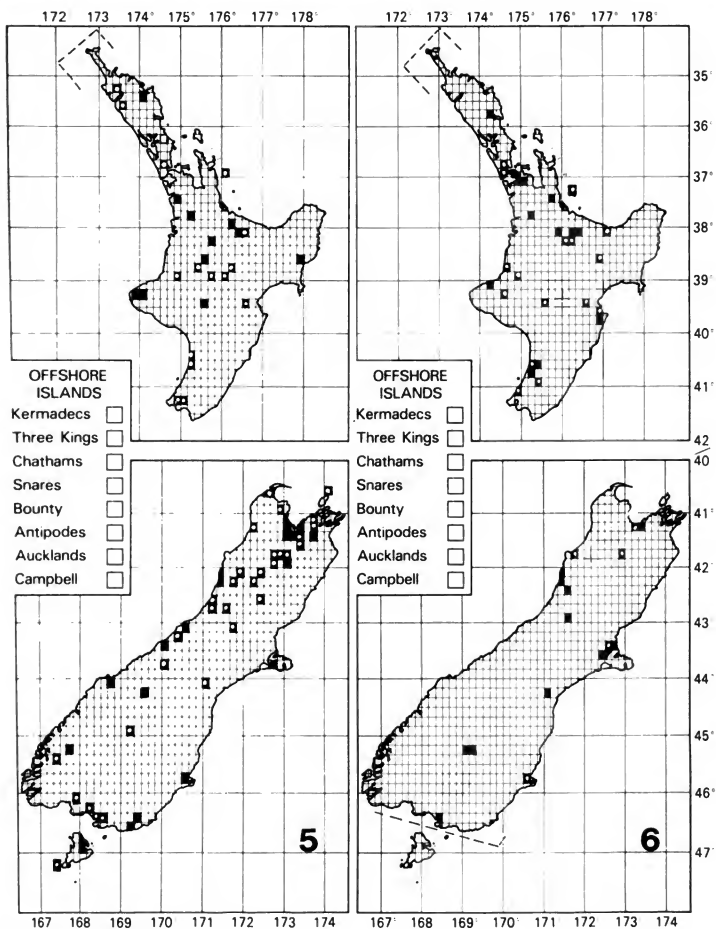


Fig. 1-8 (continued)

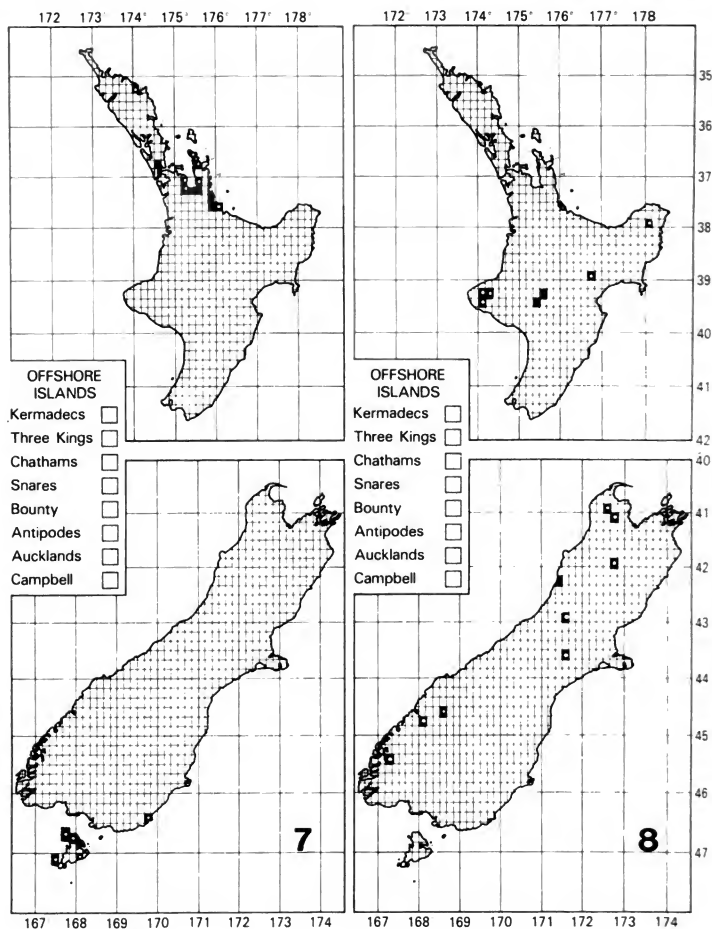


Fig. 1-8 (continued)

wings held flat in repose.

forewing termen sinuous, i.e., emarginate at apices of veins M1, M2. There are two exceptions, both with narrow pointed wings: *A. persecta* Meyrick, and *A. syntona* Meyrick. forewings with veins R4, R5 (Rs3, Rs4) separate.

The *Ctenopseustis* & *Planotortrix* subgroup is so closely approached in facies by the alpine *Gelophaula* (which has thickened male ennae, and an entire forewing termen) and by *tamacta* (which has forewing veins R4, R5 lked). Otherwise, the relatively large size, the flat wing posture, and the beak-like labial palpi superficially distinguish the subgroup.

Each genus, although definable, has species which have one or two character states always present in other three genera. For instance, the capitulum of *corpus bursae* signum is always skewed in *Planotortrix* (in the restricted sense), and is upright (g-like) in *Ctenopseustis* (e.g., Fig. 56), except for *servana* (Fig. 69), which has a skewed, *Planotortrix*-type" capitulum.

In the course of examining tortricid genera, both M. Horak (pers. comm.) and I independently served that the ovipore chamber contains eversible scales (Fig. 61, 62). In the *Ctenopseustis*–*Planotortrix* group, and in *Epiphyas* Turner there are five lobes: three large dorsal lobes directed obliquely laterally, apically truncate; short small subventral lobes; and a single, apically emarginate ventral lobe. "*Cnephasia*" *jactatana* (Walker), "*Cn*". *incessana* Walker, and species *Sparganothis pilleriana* Denis Schiff. and *Xenothictis* Meyrick from New Zealand, the five lobes are differently directed (dorsal lobes directed laterally) and the ventral lobe large, and apically simple or with a membranous process. The function of these structures has not been demonstrated.

Relatively full generic descriptions have been given for *Ctenopseustis* (Green & Dugdale 1982: 74–28) and for *Planotortrix*s.1. (Dugdale 1966a). The descriptions given below concentrate on the defining characters. As information on larval and pupal structure is at present inadequate, little is said about them in the diagnoses, except where there is earlier information.

Key to genera in the "*Ctenopseustis* *Planotortrix*" subgroup

Hindwing with a cubital pecten (Fig. 9–12); hindwing axillary cord and epaulette tufts equally large; male forewing costal fold (Fig. 23–27)

half or nearly half forewing length (and forewing with a basal transverse line of raised scales); aedeagus with orifice dorso-dextral or dextral (Fig. 28–32), 3 or more cornuti of equal length, vesica with a basal finger-like simple lobe (e.g., Fig. 28, 29); female cecum longitudinally and sinuously split, basally (i.e., at corpus bursae) expanded, twisted and inrolled (e.g., Fig. 56)

..... *Ctenopseustis* Meyrick
—Hindwing lacking a cubital pecten; male forewing costal fold one-third or less forewing length, or absent (and males with no oblique basal crest on forewing); aedeagus (Fig. 37–44) orifice dextral, dorsal or sinistral; vesica with 1 cornutus, or if with 2 or 4 cornuti, these unequal; if vesica basal lobe present, this scobinate; female cecum not split, nor basally inrolled or twisted

2 Male hindwing costal margin with a pseudofrenular tuft of long, decumbent scales hidden by a row of semi-erect pointed scales (e.g., Fig. 18, 19); female ductus bursae cecum cylindrical (not expanded basally), either collar-like and short (Fig. 77), or long and smooth, or as a sclerotised longitudinal trough (Fig. 78, 80); hindwing axillary cord and epaulette tufts equally (A. *orthopsis*) or unequally developed

..... *Apoctena* new genus
—Male hindwing costal margin unmodified (e.g., Fig. 11); female ductus bursae cecum either a flattened long tube ending well before the ductus-corporis bursae junction (Fig. 69), or a sclerotised tube with a longitudinal groove tapering from base (Fig. 64)

3 Ground colour of both sexes milky or creamy white; male forewing lacking a costal fold; axillary cord and epaulette tufts sparse, weakly developed; male aedeagus apex (Fig. 45c, lower) acuminate, orifice dorsal, vesica (Fig. 33) lacking a basal process; female cecum tubular, sclerotised, with a longitudinal invagination (groove), and evenly expanded to ductus-corporis bursae junction (Fig. 65, 67); signum with capitulum reduced

..... *Leucotenes* new genus
—Ground colour of both sexes not milky or creamy white; male forewing with a costal fold; axillary cord and epaulette tufts strongly developed; male aedeagus (Fig. 37–40) apex rounded or oblique, orifice dorso-sinistral, vesica with a basal apically scobinate process, or scobinate patch (absent in *P. puffini*); female cecum (Fig. 66, 69, 72–76) a long, often arcuate, flattened tube, signum with a well-developed, skewed capitulum

..... *Planotortrix* Dugdale

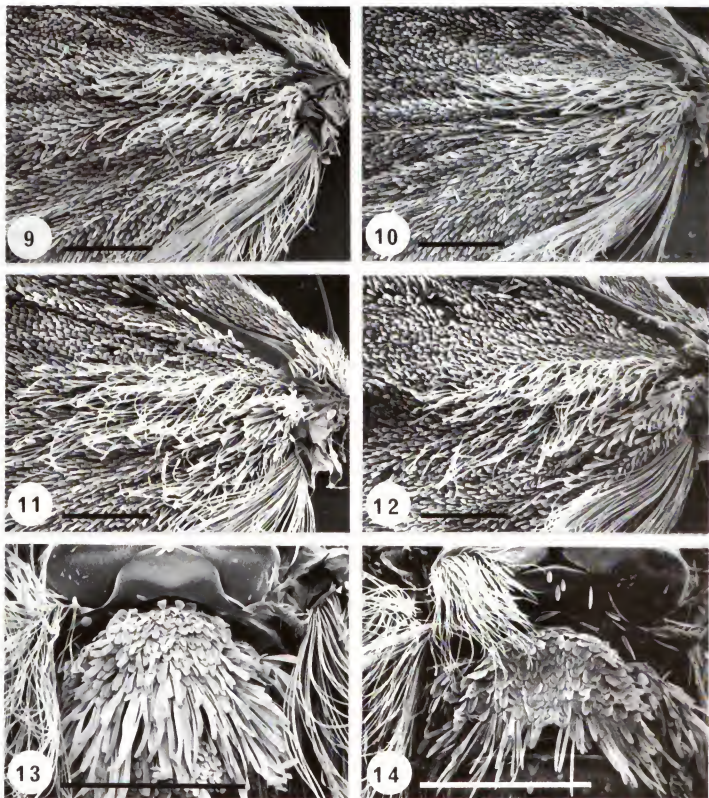


Fig. 9-14 *Ctenopseustis* species male hindwing cubital pecten detail; *Planotortrix* and *Ctenopseustis* abdomen base scaling. Scale interval = 1 mm. 9, *Ctenopseustis obliquana*, Auckland AK, male hindwing with cubital pecten (SEM prep. JSD 39); 10, *Ct. obliquana*, Nelson NN, ditto (SEM prep. JSD 40); 11, *Ct. herana*, Canaan NN, ditto (SEM prep. JSD 41); 12, *Ct. "Type II North Id"* Rukuhia WO, ditto (SEM prep. JSD 46); 13, *Ct. obliquana*, Appleby NN, abdomen base scaling (SEM prep. JSD 43); 14, *Pl. excessana* Nelson NN, ditto (SEM prep. JSD).

GNOSSES OF *CTENOPSEUSTIS* AND LUDED SPECIES

opseustis Meyrick, 1885

eyrick, 1885: 348; Green & Dugdale 1982: 427.

a species. *Teras obliquana* Walker, 1863, by
nal monotypy.

nosis. Head with the vertex scales upright,
hanging the frons, exceeding the scape; male
wing with oblique, transverse crest of scales on
l quarter, and with the costal fold (Fig. 23–27)
een 0.4X–0.5X forewing length, eversible and
floor and ceiling of the enclosed chamber
red by short tongue-like scales (Fig. 20) and
well-developed campaniform sensilla (Fig. 21);
wing with cubital pecten (Fig. 9–12) in both
s, costa arched; male with equally strong axillary
and epaulette tufts, the axillary cord tufts
indable (scale sockets 8-shaped, Fig. 15), and
nding almost to the hindwing anal angle; basal
rminal tergite with a long scale fringe (Fig. 13).
e genitalia: uncus trowel-shaped, socii very large
sclerotised on outer margin; aedeagus orifice
28–32 dorsodextral, apex acute, with 4–6
ressed spines, cornuti many (3–22), equal, needle-
; vesica basal lobe (Fig. 29, 30) slender, finger-
; unornamented, or thumb-like, obscurely
ulose (*Ct. servana* Fig. 32).

ale genitalia: colliculum ventrally split, ductus
sae smooth, tapering from bursa to three-quarters
length, thence membranous to sterigma; cestum a
sted split tube (Fig. 55–60, 63), greatly expanded
inrolled towards the ductus-corporis bursae
ation; capitulum upright (skewed in *Ct. servana*),
um with 3 arms: an invaginated dagger, a short
terior sclerotised strip, and a long slender anterior
p internally spinulose (Fig. 56, 57, 60, 63).

marks. *Ctenopseustis* differs from *Planotortrix*
l *Apoptena* nov. in its dextral aedeagal orifice,
ession of a hindwing cubital pecten, and an
olled cestum; *Leucotenes* nov. differs from
opseustis in its lack of a cubital pecten, lack of
ale forewing costal fold, and weakly developed
llary cord/epaulette tufts, but closely resembles
opseustis in the tapering dorso-dextral aedeagus
fice.

From *Epalxiphora* Meyrick (both sexes of which
o have a cubital pecten), *Ctenopseustis* differs in
ng shape, unmodified patagia, resting posture,
d lack of a subcostal field of orange, modified
les on the male hindwing, and on other characters,
ably uncus and socii structure.

Included species:

Ct. obliquana (Walker); *Ct. herana* (Felder &
Rogenhofer) revised status; *Ct. fraterna* Philpott; *Ct.*
servana (Walker); *Ct. filicis* new species. A North
Island entity, possibly of specific status, is discussed
under *Ct. herana*.

KEY TO ADULTS OF *CTENOPSEUSTIS* SPECIES

Note: The North Island pheromonally-definable
entity cannot be distinguished morphologically with
confidence from sympatric (North Island) *Ct.*
obliquana, and is not keyed.

- 1 Labial palpi usually over 3X compound eyewidth;
male uncus apex broadly rounded (Green &
Dugdale 1982, fig. 4); female with capitulum re-
duced and skewed (Fig. 70 and Green & Dugdale
1982, fig. 7); male sandy in colour, aedeagus
(Fig. 32) orifice dorsal, vesica basal lobe thumb-
like, weakly spinulose; female abdomen with
sternite 7 conspicuously dark brown scaled (Three
Kings Is, Coastal North Island and off-shore
islands) *Ct. servana* (Walker)
—Labial palpi usually 3X or less compound eye
width; male uncus apex acute (Green & Dugdale
1982, fig. 6) vesica basal lobe finger-like (Fig.
28–30); female with capitulum peg-like (Fig. 56,
57, 60, 63); male and female colour pattern
variable, but female abdomen without contrast-
ingly coloured sternite 7 scales 2
- 2 Male costal fold: forewing length ratio 1:2.2–2.4
(Fig. 26, 27); female cestum sclerotised for less
than one third total ductus bursae length (Fig. 57,
58), (South, Stewart, Chatham Islands)
..... *Ct. herana* (F&R)
—Male costal fold: forewing length ratio 1:1.9–
2.1 (Fig. 23–25); female cestum sclerotised for
over one-third total ductus bursae length or, if
cestum reduced, colour pattern yellowish or
orange fawn 3
- 3 Colour pattern distinctively yellowish or orange-
fawn with red-brown markings, underside pale
fawn with rust-red markings; male with segment
8 constricted dorso-basally; female with cestum
reduced, less than one-fifth length of ductus
bursae (Fig. 63) (Dunedin, Catlins, Bluff Hill,
Stewart Island, on *Cyathea*, *Dicksonia*)
..... *Ct. filicis* new species
—Ground colour not conspicuously yellowish-
orange fawn, and either whitish fawn, or grey, or
purple grey ventrally; male with tergite 8 not
constricted basally; female with cestum approxi-
mately half ductus bursae length 4

- 4 Ground colour dark chocolate or purplish-brown, the transverse fascia often broken in the male forewing into distinct, angular marks or (rarely) divided by a pale longitudinal band, and in the female often sharply pointed and outlined in whitish scales; male antenna lacking black scales on basal 10 segments (North Island, on *Cyathia*, *Dicksonia*, *Sticherus*) *Ct. fraterna* Philpott —Ground colour not dark chocolate or purple brown; wing pattern highly variable; male antenna with black scales on basal 10 segments (North, South Islands, polyphagous) *Ct. obliquana* (Walker)

Note: The morphological concept of North Island *Ct. obliquana* cannot differentiate *obliquana* from "Ct. Type II North Island" in the female, but there is a tendency for there to be long, hair-like scales (cf. Fig. 9, 10, 12) in the male hindwing cubital pecten in the latter entity.

Ctenopseustis obliquana (Walker), restricted (Fig. 1, 9, 10, 13, 15, 20, 21, 23, 24, 28–31, 55, 56, 60)

obliquana Walker, 1863: 302 (*Teras*) Holotype ♀ Auckland AK, A. Bolton, BMNH, abdomen missing.

spurcatana Walker, 1863: 305 (*Teras*). Holotype ♂ Nelson NN, T. R. Oxley, BMNH.

transtrigana Walker, 1863: 305 (*Teras*). Holotype ♂ Nelson NN, T. R. Oxley, BMNH, abdomen missing.

turbulentana Walker, 1863: 355 (*Sciaphila*) Holotype ♂ Nelson NN, T. R. Oxley, BMNH, abdomen missing.

ropeana Felder & Rogenhofer, 1875: pl. CXXXVII, fig. 45 (*Tortrix*) Holotype ♀ Nelson NN, T. R. Oxley, BMNH.

charactana Meyrick, 1881: 492 (*Cacoecia*) Holotype ♂ Auckland AK, E. Meyrick, BMNH, abdomen missing.

[*obliquana* Types I, III of Foster et al. 1986: 156. *obliquana* Type I of Foster & Dugdale 1988: 229]

Diagnosis. As in Green & Dugdale 1982: 430–431 fig. 3, 6, 8, 9, 12, 13 (North Island specimens) and male forewing costal fold half length of forewing (costal fold ratio 1:1.9–2.1, Fig. 23, 24); male hindwing cubital pecten (Fig. 9, 10) composed of long, sinuous capitate or strap-like scales, apically strongly decurved and appearing "curly"; anal pecten with a broad-scaled basal tuft, and long "curly" capitate scales in a strip.

Female genitalia with cestum variable (especially in South Island specimens) but usually over one-third ductus bursae length, and posterior arm of signum longer than capitulum height (Fig. 55, 56).

♀ Sex pheromone main components: Z8–14:OAc, Z5–14:OAc; North Island (Type I) ratio 80:20 (Z8:Z5, range 76: 24–84:16), South Island (Type III) ratio 90:10 (range 90:10–97:3) (Young et al. 1985; Foster et al. 1986: 156–157).

Note. Further analyses have shown that there is overlap in the ranges of ratios of pheromone components between Types I and III (Drs J. R. Clearwater, S. P. Foster, pers. comm.).

Distribution. (Fig. 1): North, South, Stewart Islands (absent from Three Kings and Chatham Islands) sea level to timberline.

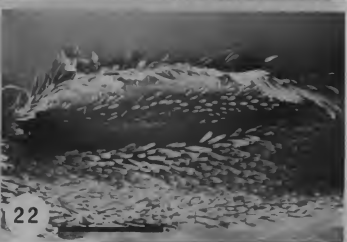
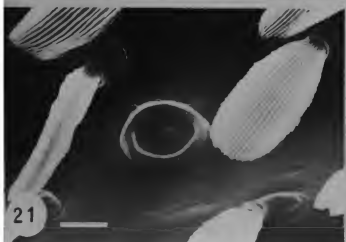
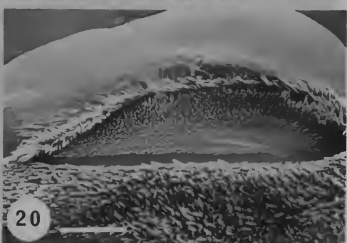
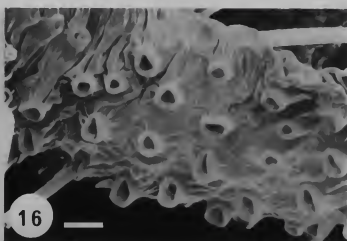
Hosts. polyphagous.

Material examined. Holotype ♂ ♂ *obliquana*, *spurcatana*, *transtrigana*, *turbulentana*, *ropeana*, Holotype ♀ *charactana* (BMNH), and 1504 additional specimens (NZAC).

Remarks. As there is no evidence of a *Ctenopseustis* species producing solely Z5–14:OAc at Auckland, I assume that the females collected by Bolton in 1854 and Meyrick in 1881 are conspecific with the 1980+ populations on which Green & Dugdale (1982) and which Foster et al. (1986) and Foster & Dugdale (1988) based their descriptions and pheromone analyses, respectively.

The synonymy involving *spurcatana*, *transtrigana*, *turbulentana*, and *ropeana* is based on costal fold/forewing length ratios of the four holotype males. All fall within the range of ratios 1:1.9–2.1, and all have the cubital pecten curly. Because of the

Fig. 15–22 Wing structures, *Apoctena* n. gen., *Ctenopseustis*, and *Planotortrix* species. Fig. 20, 22 by kind permission of J. R. Clearwater. Scale interval = 1 mm, except where stated otherwise; 15, *Ct. obliquana*, Appleby NN, axillary cord scale sockets (SEM prep. JSD 43). Scale interval = 0.1 mm; 16, *P. excessana*, Nelson NN, ditto (SEM prep. JSD 44) Scale interval = 10 µm; 17, *Apoctena orthopsis* (Meyrick), Titirangi AK ditto, (SEM prep. JSD 47). Scale interval = 10 µm; 18, *A. orthopsis*, Titirangi AK, pseudofrenular scaling; 19, *A. conditana*, Nelson NN, pseudofrenular scaling; 20, *Ct. obliquana*, male costal fold opened out; note the diverse scale types, and relatively dense scaling; 21, *Ct. obliquana*, male costal fold, vein Sc campaniform sensillum, ×1500 magnification. Scale interval = 10 µm; 22, *P. excessana*, male costal fold opened out; note sparse scaling.



discovery of an entity in the North Island with pheromone and isozyme characteristics of *Ct. herana* and the morphology of *Ct. obliquana*, Fig. 1 combines distribution records of specimens that combine *Ct. obliquana* morphology. Fig. 2 shows the distribution of known populations of the *Ct.* "Type II North Island" entity, based on analyses of females or on the capture of males in Z5-14:OAc baited traps. This entity is discussed further under *Ct. herana*.

Ctenopseustis herana (Felder & Rogenhofer)

Reinstated species

(Fig. 2, 11, 26, 27, 57, 58)

herana Felder & Rogenhofer, 1975: pl. CXXXVII, fig. 52 (*Tortrix*) Holotype ♂ Nelson NN, T. R. Oxley, BMNH, abdomen missing.

inana Butler, 1877: 403, (pl. 43, fig. 13 (*Cacoecia*) Holotype ♀ "Canterbury" J. D. Enys, BMNH, genitalia slide no. 10609.

[*obliquana* Type II of Foster et al. 1986: 1565, Foster & Dugdale 1988].

Diagnosis. Male with forewing costal fold less than half as long as forewing (ratio 1:2.2-2.4, Fig. 26, 27), male hindwing cubital pecten composed of slender, more or less straight, uniform or strap-like scales, and the pecten extending beyond halfway towards the base of vein CuA1 (Fig. 11).

Female with cestum variable (Fig. 57, 58), but usually less than one-third ductus bursae length, and posterior arm of signum (Fig. 57) not longer (often shorter) than capitulum height.

♀ Sex pheromone main component: Z5-14:OAc (Foster et al. 1986: 156; Foster & Dugdale 1988: 229).

Distribution: (Fig. 2): South, Stewart, and Chatham Is (excluding Rangatira Island), sea level to timberline.

Hosts. polyphagous.

Material examined: Holotype ♂ *herana* (BMNH), Holotype ♀ *inana* (BMNH), and 503 specimens (NZAC).

Remarks. The holotype male of *Tortrix herana* has a costal fold:forewing length ratio of 1:2.26, and the hindwing cubital pecten is composed of more or less straight hair-like scales. Females from the Dun Mountain Track by Nelson City, and from Appleby research orchard at the seaward foot of the Moutere Hills (NN), which on analysis of pheromone content yielded only Z5-14-OAc agreed in cestum and signum characters with Z5-14:OAc producing

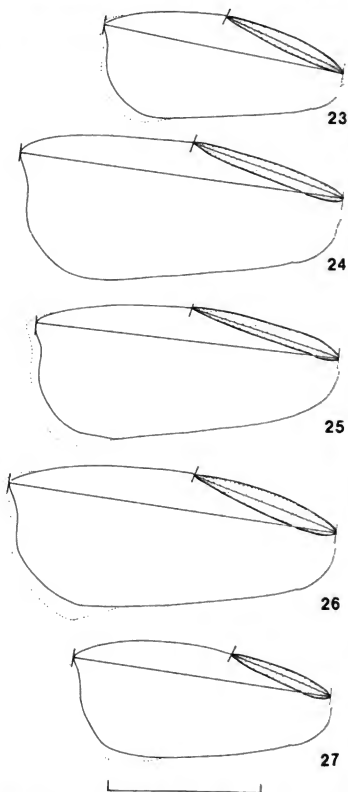


Fig. 23-27 *Ctenopseustis* species, male costal fold:forewing length ratio measurement sites, and wing shape; 23, *Ct. obliquana*, Auckland AK; 24, *Ct. obliquana*, Oban SI; 25, *Ct.* "Type II North I", Rukuhia WO; 26, *Ct. herana*, Canaan N.N; 27 *Ct. herana*, Tai Tapu MC.

females from Christchurch and nearby Taitapu (MC), the presumed area where J. D. Enys may have collected the female described by Butler as *Cacoecia inana*. The holotype female of *C. inana* also agrees

cestum sclerotisation length and the posterior arm of the signum in *Ct. herana*, i.e., the combination of long cestum and long posterior signum arm" was not observed.

This concept of *Ct. herana* has not been recorded from the North Island. It is largely sympatric with *Ct. obliquana* in the South and Stewart Islands, except for the Canterbury Plains around Christchurch (which only *Ct. herana* is known (but both species are present on the contiguous Banks Peninsula) and the Clutha-Kawarau-lower Manuherikia valley floors (i.e. "Central Otago orchard area") from which only *Ct. obliquana* is known.

Ctenopseustis "Type II North Island" (fig. 2, 12, 25, 59)

Material examined. 23 ♂♂ 12 ♀♀ (NZAC)

In terms of female-produced long-range sex pheromone components, selected isozymes, and, under confined conditions, captures of (South Island) *Ct. herana* males in sticky traps baited with *Ct.* "Type II North Island" females in a field cage, *Ct.* "Type II North Island" must be included in the species *Ct. herana*. Although the amount of Z5-14:OAc in pheromone glands of North Island females was observed to be less, on average, than in South Island males, the ranges of quantities observed overlapped (P. Foster, pers. comm.).

In terms of morphology – male costal fold length relative to forewing length (Fig. 25) and male hindwing pecten scaling (Fig. 12), *Ct.* "Type II North Island" is not consistently distinguishable from *Ct. obliquana*, with which it is known to be sympatric at Rukuhia ND, and Rukuhia (WO).

Fig. 2 gives the known distribution (two localities used on analysis of females, one on incidence of males in traps baited with Z5-14:OAc. As *Ct. obliquana* and *Ct.* "Type II North Island" are not consistently morphologically distinguishable, the distribution shown for *Ct. obliquana* (Fig. 1) may well include specimens morphologically *obliquana* exhibiting pheromone and isozyme characters of *herana*.

Interpretation of the status of the entity *Ct.* "Type II North Island" cannot progress without more rigorous comparative studies on, for example, incidence of intersexes and developmental synchrony between male and female progeny of reciprocal crosses with *Ct. herana* (South Island), (b) mitochondrial DNA studies, (c) a wider spectrum of enzymes, with these analyses covering more populations.

Until such information is available, the entity *Ct.* "Type II North Island" is here objectively regarded as an example of parallelism, this being the least restrictive assumption, in the sense of Throckmorton (1965: 228). This entity displaying the morphology of one species with which it is sympatric, and the chemical sexual communication system (at least in large part) and part of the isozyme pattern of another allopatric species, may well be of interest in speciation studies.

Ctenopseustis fraterna Philpott (Fig. 3)

fraterna Philpott, 1930: 7. Holotype ♂ (designated by Philpott) Whangarei ND, C. E. Clarke, AMNZ. ———, Green & Dugdale 1982: 428, 435, fig. 5 (♂ genitalia), 11 (♂), 15(♀), 19(♂ hindwing pecten) (redescription).

Diagnosis. As in Green & Dugdale 1982: 435, fig. 5, 11, 15, 19, and male forewing costal fold: forewing length ratio 1:1.8–2.0. Hindwing cubital pecten composed of loosely curled strap-like scales. Lowland specimens (localities below 300 m) as in Green & Dugdale 1982, upland specimens (localities over 300 m) more transversely marked, transverse markings strongly toothed, and often outlined in silver-grey scales. Female cestum over one-third ductus bursae length (0.5×–0.6× bursa length, Green & Dugdale 1982).

♀ Sex pheromone main components: not identified; possibly consisting of various tetradecadienyl acetates. (Dr S. P. Foster, pers. comm.)

Distribution (Fig. 3). North Island only.

Hosts. Pteridophyta: *Cyathea dealbata*, *C. smithii*; *Dicksonia fibrosa*, *D. squarrosa*; *Sticherus cunninghamii* (to 1100 m).

Material examined. Holotype ♂ *fraterna* (AMNZ); and 126 additional specimens (NZAC).

Remarks. The dark chocolate or purplish, or contrastingly chocolate/orange brown/ash colour patterns are distinctive; at rest *Ct. fraterna* blends with the dead fronds of its hosts, all of which are ferns. One male reared from *Sticherus* has the proximal half of the forewing disc pallid, forming a pale saddle-shaped mark also seen in some males of *Ct. obliquana* and *Ct. herana*. The long costal fold in the male, and the relatively long female cestum may point to closer affinity with *Ct. obliquana* than with *Ct. herana*.

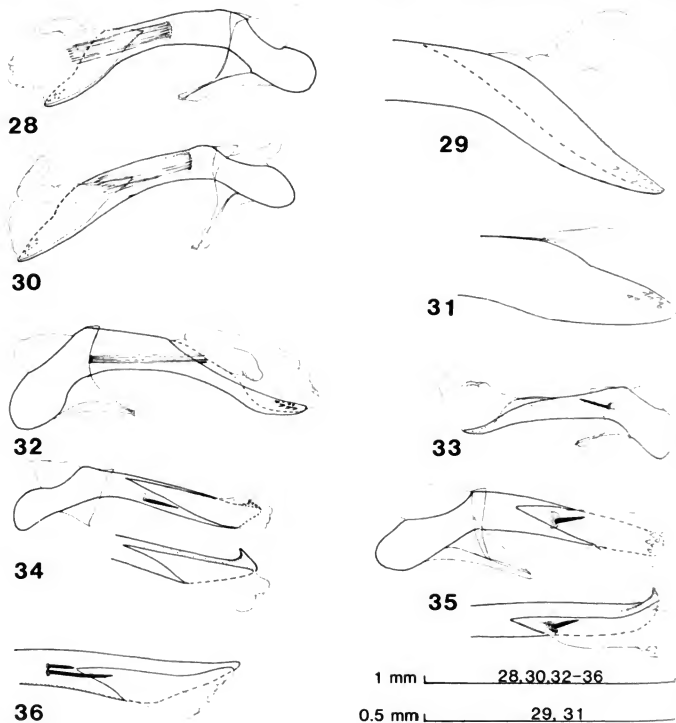
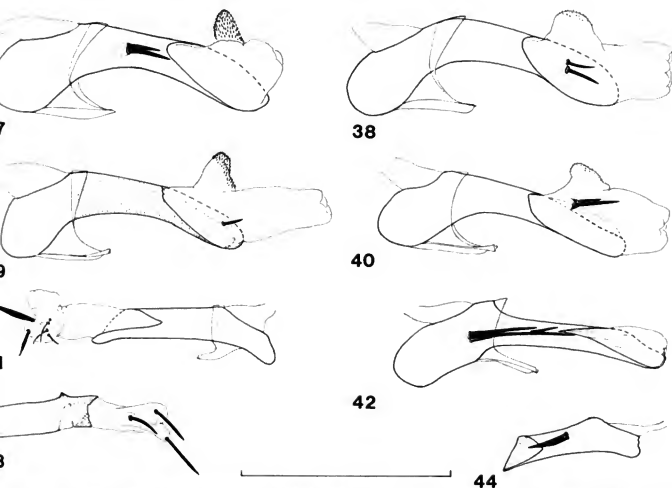


Fig. 28–36 *Ctenopseustis*, *Leucotenes*, *Planotortrix* species, aedeagal structure; 28, *Ct. obliquana*, Auckland AK right aspect; 29, ditto, vesica and aedeagus apex, left aspect; 30, *Ct. obliquana*, Appleby NN, right aspect; 31, ditto, vesica and aedeagus apex, left aspect; 32, *Ct. servana*, Mangawhai Heads ND, left aspect; 33, *Leucotenes coprosmae*, Tarrarua Range WN, right aspect; note single cornutus (cf. Fig. 45); 34, *Planotortrix flammea*, Homer Tunnel FD, left aspect; insert, aedeagus apex dorsal view; 35 *P. notophaea*, Manurewa AK, left aspect; insert, aedeagus apex, dorsal aspect; 36 *P. puffini*, Lee Bay SI, aedeagus apex, dorsal aspect.



37–44 *Planotortrix* and *Apoctena* species, aedeagal structures.; 37, *P. excessana*, Dun Mountain, Nelson NN, left aspect; 38, *P. avicenniae*, Kopu WO/CL, left aspect; 39, *P. octo*, Auckland (laboratory colony), left aspect; 40, *P. pseudocto*, Chatham Is, left aspect; 41, *Apoctena conditana*, Opouri Valley SD, right aspect; 42, *A. orthopis*, Taranaki WN, left aspect; 43, *A. pictoriana*, Craigieburn Forest Park, MC, left aspect; 44, *A. flavescens*, Beaumont Forest, right aspect.

tenopseustis filicis Dugdale, new species
(figs 3, 63, 71)

tenopseustis Type IV of Foster et al. 1986, Foster & Dugdale 1988.]

Description. Colour pattern variable, largely reddish brown on a yellow-fawn or warm ochreous ground; underside of body and hindwings pallid, sometimes cream-coloured, particularly in females. Wingspan: 19–24 mm (♂♂), 22–28 mm (♀♀). Males with anal fold; forewing length ratio as for *Ct. obliquana* 1.9–2.1; and abdomen with segment 8 constricted meso-basally, and tergite 8 expanded apically, forming a hood; (Fig. 71). Female with cestum very reduced, less than one-quarter total ductus bursae length, and posterior arm of signum not longer than pitulum height (Fig. 63).

Sex pheromone main components: Z10–16:OAc, 4–14:OAc (Foster & Dugdale 1988: 229).

Hosts. Pteridophyta: *Dicksonia squarrosa* (favoured SL, SI sites);

Cyathea smithii (favoured in DN sites; on both young (soft) and older (hardened) fronds).

Holotype ♂ New Zealand SL Bluff Hill Glory Track, larva coll. 8 March 1986 J. S. Dugdale & J. R. Clearwater “ex *Dicksonia*, em. 30.6.86” NZAC, wing span 19 mm.

Material examined. Holotype ♂, allotype ♀ same data as Holotype except “em. 15.6.86”, and 84 additional specimens, NZAC.

Distribution (Fig. 3). DN: Leith Saddle (reared ex *Cyathea*); SL: Rangleburn State Forest (to light); Chaslands, Tautuku State Forest (reared ex *Dicksonia*), Tisbury, West Plains, Bluff (to light, A. Philpott), Bluff Hill (reared); SI: Oban area, (to light; reared ex *Dicksonia*, *Cyathea*; in baited sticky traps) at Raroa Track, Horseshoe Bay, Lee Bay, Observation Rock.

Remarks. This conspicuous orange-brown species with its rust-red or red-brown markings and pale, cream, or buff venter and hindwings was first

recognised as a species by analyses of pheromone components. *Ct. filicis* is the most geographically restricted *Ctenopseustis* species, and unlike *Ct. fraterna*, it has not been reared from host ferns other than the two listed species. In facies (broad wings, long costal fold, colour pattern elements) it is very similar to *Ct. obliquana*, but the female genitalia resemble those of *Ct. herana* (reduced cestum and posterior arm of signum). The female-produced sex pheromone components suggest an affinity with *Ct. obliquana* as there is no trace of Z5-14:OAc and the preponderant Z10-16:OAc is probably produced along a similar biosynthetic pathway as shown for Z8-14:OAc (Foster & Roelofs 1988: fig. 3).

The name *filicis* is the genitive singular of the noun *felix* = fern (Latin), and refers to the larval hostplant.

Ctenopseustis servana (Walker)

(Fig. 4, 32, 61, 64, 70)

servana Walker, 1863 (*Teras*) Holotype ♂ Auckland AK, A. Bolton, BMNH, abdomen missing. Synonymy as in Green & Dugdale 1982: 431; Dugdale 1988: 121.

Diagnosis. As in Green & Dugdale 1982: 428, 431, fig. 4, 7, 10, 14, 18. Male costal fold: forewing length ratio 1:2.2-2.3; male hindwing cubital pecten composed of hair-like scales, and fringe of abdominal tergite 1 weakly developed (strongly so in other *Ctenopseustis* species); uncus apex rounded-truncate; aedeagus orifice dorsal, basal lobe on vesica short, weakly spinulose apically (Fig. 32). Female with capitulum of signum skewed (obliquely bent), anterior and posterior signum arms equal in length (Fig. 64, 70).

♀ Sex pheromone main components: Z5-14:OAc, ratio range 32:68-35:65 (Foster & Dugdale 1988: 229).

Distribution (Fig. 4). North Island: off-shore islands, Three Kings Islands, coastal ND, AK, CL, WO, TK, WI-WN; absent from coastal BP, GB, HB, and WA.

Hosts. polyphagous on woody coastal angiosperms.

Material examined. HT ♂ *servana* and 144 additional specimens (NZAC).

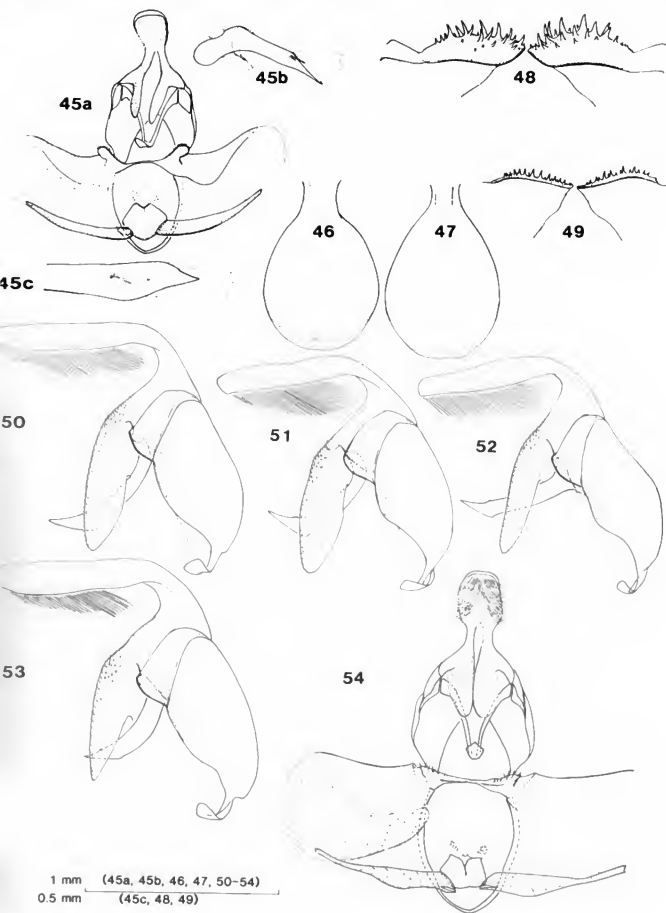
Remarks. *Ct. servana* is the only *Ctenopseustis* species recorded on the Three Kings Islands. It has not yet been found more than 2 km inland in the North Island. The very long palpi, the skewed capitulum, the rounded uncus apex, the thumblike, scobinate vesica process, and the combination of Z5-14:OAc and Z7-14:OAc in the female-produced sex pheromone are character states more commonly found in *Planotortrix*. Some *Ctenopseustis* character states are reduced: the line of raised scales on the forewing, the conspicuous fringe on abdominal tergite 1, the cubital pecten. The aedeagus, however, has a dorso-dextral orifice (Fig. 32), and the cestum is expanded and inrolled at the ductus-corporis bursae junction (Fig. 64, 70).

Leucotenes Dugdale, new genus

Type species. *Planotortrix coprosmae* Dugdale, 1988.

Description. Labial palpi porrect, over twice compound eye width, vertex scales exceeding scape height, vertex scale tufts not divergent, mesoscutellum lacking a crest, forewing termen emarginate at veins M1, M2, male forewing lacking a costal fold, and without a line of raised scales on basal third, hindwing costa unmodified, cubital pecten absent, axillary cord and epaulette tufts weakly scaled; abdominal tergite 1 lacking a long scale fringe; male genitalia (Fig. 33, 45) with socii shorter than gnathos arms, transtilla with teeth congested, and not in a single row; aedeagus expanded subapically, tapering to an acuminate apex, vesica dorso-apical, with one cornutus or two unequal cornuti. Female genitalia (Fig. 62, 65, 67) with cestum evenly sclerotised with a very long groove or trough, and widened to junction with corpus bursae, capitulum (Fig. 65) reduced, anterior and posterior signum arms reduced, dagger present, either stout and short (Fig. 65) or long (Fig. 67).

Fig. 45-54 *Leucotenes*, *Planotortrix*, *Apoctena* species, male genitalia; 45, (a) *Leucotenes coprosmae*, Prices Valley Bush MC, male genitalia; (b) (top insert), aedeagus, left view; (c) (bottom insert), aedeagus apex, ventral; note presence of 2 cornuti (cf. Fig. 33); 46, *Planotortrix excessana* Dun Mtn NN, uncus dorsal view; 47, *P. octo*, Tai Tapu MC, uncus dorsal view; 48, *P. octoides*, Pitt Island, Chatham, transtilla, posterior view; 49, *P. avicenniae*, Kopu WO/CL, transtilla, posterior view; 50, *P. excessana*, Dun Mtn NN, tegumen, uncus, gnathos, socii, lateral view; 51, *P. octo*, Tai Tapu MC, ditto; 52, *P. octoides*, Pitt Island, Chatham, ditto; 53, *P. avicenniae*, Kopu WO/CL, ditto; 54, *Apoctena conditiana*, Opouri Valley SD, male genitalia, posterior view.



Remarks. *Leucotenes* is distinguished from *Planotortrix* (cf. Dugdale 1966a: 396, as *Planotortrix charactana*; Dugdale 1988: 125 as *Planotortrix coprosmae*) by the lack of strongly-scaled axillary cord and epaulette tufts, the reduced socii, the spear-like aedeagus apex, and the form of the cestum. From *Ctenopseustis* (which it resembles in colour pattern and facies) *Leucotenes* is distinguished by the absence of a hindwing cubital pecten and the forewing costal fold, the reduced socii, lack of spines on aedeagus apex, one or two stout cornuti, rather than several fine cornuti, lack of a basal lobe on the vesica, the reduced signum, the straight cestum invagination, and cestum extending to four-fifths ductus bursae length. This last character, and the absence of a pseudo-frenulum on the male hindwing, distinguish *Leucotenes* from *Apociena* described below.

The combination of facies, colour pattern, and aedeagus shape suggest a relationship with *Ctenopseustis*.

Leucotenes is monobasic and restricted to New Zealand, where the only species is widely distributed, with members of the shrub genus *Coprosma* (Rubiaceae) as hosts.

Etymology. The name is derived from the Greek *leukos* = white, and *tenes*, a conventional suffix for tortricids, feminine.

***Leucotenes coprosmae* Dugdale**
(Fig. 33, 45, 62, 65, 67)

coprosmae Dugdale, 1988: 125 (*Planotortrix*; as new name for *Tortrix*)

charactana nec Meyrick, 1881: 492. Holotype ♂, Christchurch MC, E. Meyrick, BMNH, BM, genitalia slide no. 8914 ♂.

charactana, Meyrick 1883: 50–51 (*Tortrix*); ———, Hudson 1928: 227, pl. XXIV fig. 33–35 (description and colour illustration) ———, Philpott 1928: 450–451, p. 465 fig. 60 (male genitalia) ———, Dugdale 1966a: 396 (in *Planotortrix*).

Diagnosis. As illustrated by Hudson 1928, pl. XXIV, fig. 33–35; wing span variable, 14–18 mm (AK), or 18–20 mm (SL) to 24–26 mm (subalpine WN, NN). Ground colour of head, thorax, forewings, and abdomen creamy or milky white; forewing invariably (137 specimens) with a short oblique black, chocolate, or dark red bar on the costa at just under half costal length, rest of the "tortricoid" wing pattern faintly

(lowland specimens) to strongly (upland and timberline specimens) developed. Aedeagus (Fig. 33, 45) sharp pointed, the longer cornutus less than one-quarter length of the aedeagus, the other, when present, half the length of the first. Female genitalia (Fig. 62, 65, 67) as for generic description; signum dagger short and stout or long and slender.

♀ **Sex pheromone main components:** Calling pheromone: Z11–14:OAc (S.P. Foster, pers. comm.)

Distribution. North, South, and Stewart Islands, throughout; sea level to timberline.

Hosts. small-leaved species of *Coprosma* (Rubiaceae).

Larva. Body distinctively green, with a red dorsal stripe more or less as figured by Hudson 1928, pl. iii fig. 17.

Material examined. Holotype ♂ *coprosmae* (BMNH); and 136 specimens (NZAC).

Remarks. Differences in cornutus-number (Fig. 33, 45) and cestum base shape (Fig. 65, 67) suggest that there may be more than one entity lumped under *charactana*.

***Planotortrix* Dugdale, restricted**

Planotortrix Dugdale, 1968: 292

[*"Planotortrix I"* of Foster & Dugdale 1988: 229]

Type species. *Teras excessana* Walker, 1963 by original designation.

Diagnosis. Head with vertex scales proclinate short and exposing the frons. Male forewing with costal fold 0.4× or less forewing length, and floor and ceiling of the chamber enclosed by the fold with a sparse field of short broad scales (Fig. 20). Male forewing smooth-scaled. Both sexes with labial palpi elongate triangular. Hindwings lacking a cubital pecten; anal pecten in both sexes with hair-like scales, axillary cord and epaulette with hair-like scales extending to three-quarters or less the distance to the hindwing anal angle, axillary cord scale sockets either not 8-shaped (*flammea*, *excessana* groups), (Fig. 16) or 8-shaped (*notophaea* group). First abdominal tergite (Fig. 14) weakly fringed. Male genitalia with aedeagus orifice dorso-sinistral, 1 or 2 cornuti, short, unequal, apex rounded; vesica often with thumb-like, scobinate basal lobe. Female genitalia with the cestum a long, flattened tube, sometimes with the strongest sclerotisation restricted to one side, and signum with capitulum decumbent and smooth, anterior signum arm weakly developed, with few, weak spinules.

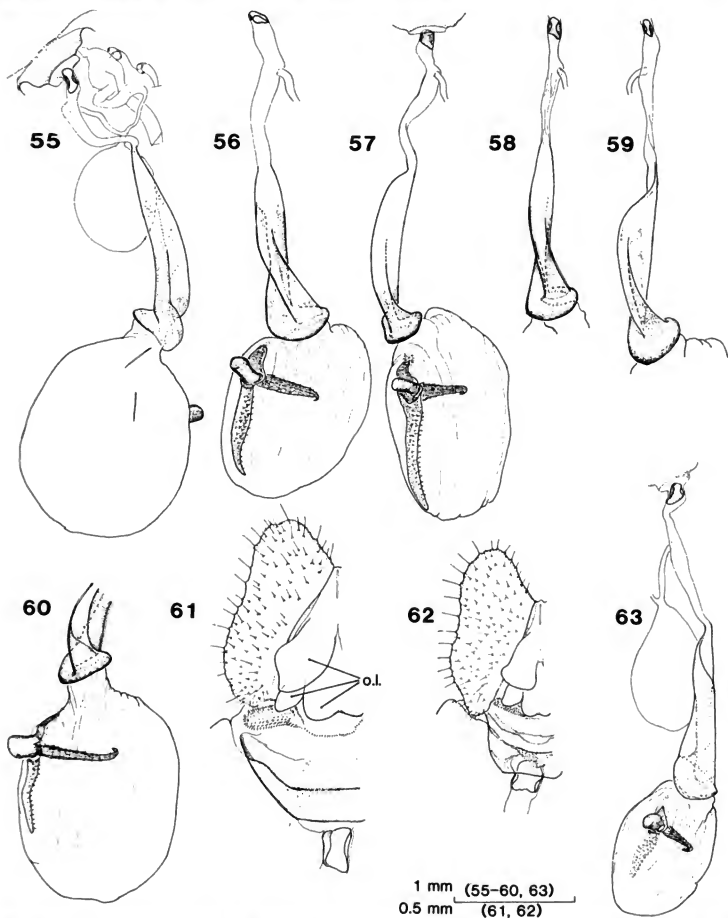


Fig. 55–63 *Ctenopseustis* and *Leucotenes* species, female genitalia; 55, *Ctenopseustis obliquana*, Waitakere Ranges, AK; 56, *Ct. obliquana*, Manurewa AK ("♀" 341, single tip analysis); 57, *Ct. herana*, Dun Mtn NN ("♀" WCC 19 single tip analysis); 58, *Ct. herana*, Appleby NN ("♀" 81, single tip analysis), ductus bursae; 59, *Ct.* "Type II North I." Rukuhia WO, ductus bursae; 60, *Ct. obliquana*, Waitakere Ranges AK, ductus bursae base, bursa, and signum; 61, *Ct. servana*, Manaia TK, sterigma, papillae anales, and oviporal eversible lobes (OL); 62, *Leucotenes coprosmae*, Lake Rotoiti BR, ditto; 63, *Ct. filicis*, Lee Bay SI, corpus and ductus bursae.

Remarks. *Planotortrix* differs from *Ctenopseustis* in lacking a cubital pecten, the male costal fold covering a sparsely scaled chamber often with reduced campaniform sensilla; and, in both sexes, by the short, proclinate vertex scales which do not overhang the frons. The female genitalia have a flattened cestum, quite unlike the in-rolled, split, twisted cestum characteristic of *Ctenopseustis*, or the grooved tube of *Leucotenes*. From *Apoctena*, *Planotortrix* is distinguished by the unmodified hindwing costal margin and its flattened, rather than tubular, cestum. The long porrect palpi and broad forewings give *Planotortrix* a distinctive facies; from the superficially similar *Catamacta* the genus is distinguished by the forewing veins R4 and R5 (RS3 and RS4) arising separately from the discal cell, and the larger overall size (*Planotortrix* species wingspan is usually over 18 mm, generally over 24 mm; *Catamacta* species rarely exceed 16 mm).

Included species:

P. excessana (Walker); *P. avicenniae* new species; *P. flammea* (Salmon); *P. notophaea* (Turner); *P. octo* new species, *P. octoides* new species; *P. puffini* new species.

KEY TO ADULTS OF *PLANOTORTRIX* SPECIES

- 1 Male costal fold with a field of scattered broad scales on the "ceiling"; uncus beak trowel-shaped (apically blunt); no basal process on the vesica; aedeagus apex acute or with a lateral process or horn; female cestum sclerotised laterally only (*notophaea* complex) 2
—Male costal fold lacking broad scales on the "ceiling" (Fig. 20); uncus beak paddle-shaped (apically broadly rounded, Fig. 46, 47); vesica with a thumb-like process, aedeagus apex broadly rounded; female cestum broadly sclerotised (*excessana* complex) 4
- 2 Purple-brown or orange-brown moths with whitish hindwings and abdomen, hindwings with a conspicuous purple fringe; male costal fold: forewing length ratio 1:3.2–3.6, hindwing axillary cord tuft extending only halfway to anal angle of hindwing; aedeagus with apical thorn, vesica

lacking strong spinules (Fig. 34); female cestum curved with two lateral sclerotised strips (Fig. 73) (larva on *Hebe* spp., GB-FD)

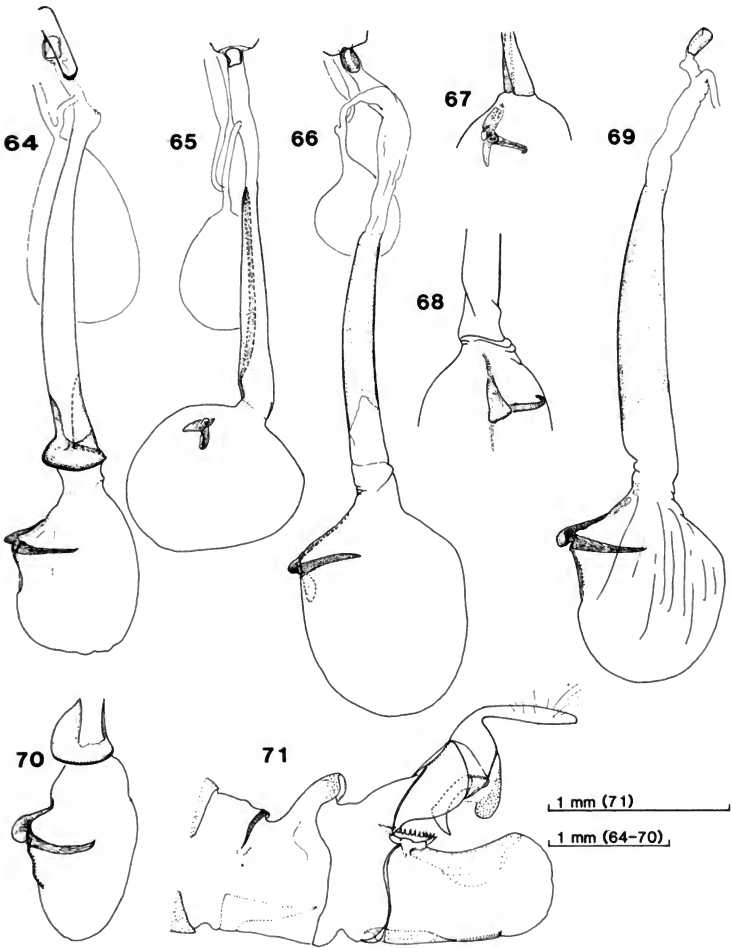
..... *P. flammea* (Salmon)
—Hindwings, if whitish, without a contrasting purple fringe; male costal fold:forewing length ratio 1:2.5–2.7; abdomen in both sexes often with a black lateral stripe; male axillary cord tuft strong and extending close to hindwing anal angle; aedeagus apex acuminate, directed diagonally or at right angles to long axis (Fig. 35, 36); female cestum sclerotised along one lateral margin (Fig. 74, 75) 3

- 3 Robust moths, wingspan generally exceeding 22 mm, often over 30 mm (especially females); male hindwing anal pecten with hair-like scales; vesica with 2 cornuti (Fig. 36), vesica lacking basal spinules; female cestum widest posteriorly (Fig. 75) (larva on large-leaved Asteraceae, FD, SL coastal, SI coastal, and subalpine)

..... *P. puffini* new species
—More streamlined moths, wingspan not exceeding 20 mm, usually 15–18 mm; male hindwing anal pecten of stiff, narrow strap-like scales with bifid apices; abdomen in both sexes with a black lateral stripe; vesica with 1 stout cornutus, vesica base with a patch of 3–10 broad sclerotised spinules (Fig. 35); female cestum widest at half length (Fig. 74) (larva polyphagous, Three Kings ND-SI, coastal to montane)

- 4 Male socii in lateral view narrow and pointed (Fig. 52, 53); basal lobe of vesica obscurely scobinate (at $\times 32$ magnification) (Fig. 38, 40); larvae brown-headed (head capsule sclerotised and patterned, prothoracic and anal shields sclerotised, body grey-green with contrasting pale setal pinaculae) 5
—Male socii in lateral view broad, apically rounded (Fig. 50, 51); basal lobe of vesica strongly scobinate (at $\times 532$ magnification); larvae green-headed (head capsule greenish, prothoracic and anal shields concolorous with body, integument usually with a whitish "bloom") 6
- 5 Female cestum scarcely sclerotised and then only on the middle third of the expanded portion

Fig. 64–71 *Ctenopseustis*, *Leucotenes*, and *Planotortrix* species, female genitalia, *Ctenopseustis filicis* male genitalia; 64, *Ctenopseustis servana*, Great I, Three Kings Is; 65, *Leucotenes coprosmae*, Lake Rototoi BR; 66, *Planotortrix avicenniae*, Matakana I. BP; 67, *L. coprosmae*, Lake Rototoi BR, corpus/ductus bursae junction, signum; 68, *P. avicenniae*, Matakana I. BP, corpus/ductus bursae junction, signum; 69, *P. excessana*, Appleby NN (\varnothing 48 single tip analysis); 70, *Ct. servana*, Manaia TK, ductus corpus bursae apex, corpus bursae; 71, *Ct. filicis*, Oban SI, male postabdomen, lateral view showing dorsally constricted segment 8.



of the ductus bursae, capitulum peg-like, rounded (Fig. 76); male transtilla teeth on a stout ridge, congested and irregularly triseriate, aedeagus orifice with dextral margin unsclerotised (Fig. 40); male costal fold: forewing length ratio 1:2.9–3.5; colour pattern of both sexes variable; larva polyphagous (Chatham Is)

.....*P. octoides* new species

—Female cestum sclerotised over most of the expanded portion of the ductus bursae, capitulum flattened or depressed (Fig. 66); male transtilla teeth on a narrow ridge, largely uniseriate (Fig. 49), aedeagus orifice dextral margin sclerotised (Fig. 38); male costal fold: forewing length ratio 1:2.5–2.7; colour pattern of both sexes usually charcoal or dull brown, pattern elements often picked out with ash or cream scales; larva on *Avicennia*, ND, AK–BP, estuarine

.....*P. avicenniae* new species

- 6 Male costal fold: forewing length ratio 1:2.9–3.3; expanded portion of uncus almost as wide as long (Fig. 46), aedeagus orifice dextral margin sclerotised. (Fig. 37); female cestum sclerotised over three-quarters of its length, no lateral, longitudinal shallow groove (Fig. 69); larva polyphagous, ND–SI*P. excessana* (Walker)
—Male costal fold: forewing length ratio 1:2.6–2.7; expanded portion of uncus clearly longer than wide (Fig. 47), aedeagus orifice dextral margin unsclerotised (Fig. 39); female cestum usually sclerotised over entire length, and often with a shallow groove along one side, widest posteriorly (Fig. 72); larva polyphagous, ND–SL

.....*P. octo* new species.

Note: The morphological and colour pattern overlap between adults of all members of the *excessana* complex (key couplets 4–6) makes identification of wild-caught adults—especially females—uncertain. One species can be distinguished geographically (*P. octoides*, the only known Chatham species in the complex) and another species can be distinguished by the range of its host plant, (*P. avicenniae* on mangrove). Both of these have “brown-headed” larvae. Females of the two species that have “green-headed” larvae cannot always be confidently distinguished; males can be distinguished on costal fold: forewing length ratios, and, less easily, on uncus shape and aedeagus apex sclerotisation. Each species in the *excessana* complex has a distinctive female-produced sex pheromone.

Planotortrix excessana (Walker)
(Fig. 5, 14, 16, 22, 37, 46, 50, 69)

excessana Walker, 1863: 303 (*Teras*). Lectotype ♂, Nelson, NN, T. R. Oxley, BMNH.

biguttana Walker, 1863: 305 (*Teras*) Lectotype ♂, Nelson, NN, T. R. Oxley, BMNH

[“*Planotortrix* Type B” of Foster et al. 1986: 156, “*Planotortrix* Types B & C” of Foster & Dugdale 1988: 229. “*Planotortrix excessana*” of Foster et al. 1989: 457–465].

Diagnosis. Wingspan ranging from 19–28 mm (males) and 22–34 mm (females).

Male costal fold: forewing length ratio 1:2.9–3.3; male uncus paddle-shaped, expanded area almost as wide as long (Fig. 46), socii in lateral view 2× wider than gnathos arms, and sclerotised in a strip along the caudal margin (Fig. 50); vesica with 2 cornuti, scobinations on the vesica basal lobe easily visible at ×32 magnification (Fig. 37). Female ductus bursae with cestum broadly and strongly sclerotised on all but the basal quarter, and widened from posterior to anterior (Fig. 69).

♀ calling pheromone main components: Z5–14:OAc, ratios ranging from 3:97–71:29, (Z5:Z7), and Z9–14:OAc (Foster & Dugdale 1988; Foster et al. 1989).

Distribution (Fig. 5). ND–SI, locally absent on Canterbury Plains around Christchurch, and part of Central Otago; sea level to montane forest.

Hosts. Polyphagous (excluding ferns, and small-leaved angiosperms/conifers).

Material examined. Lectotype ♂ ♂ *excessana*, *biguttana* (BMNH), and 498 additional specimens (NZAC).

Remarks. The Lectotype ♂ ♂ of *Teras excessana* and *T. biguttana* have costal fold: forewing length ratios falling within the range of males associated with females known to produce Z5–14:OAc and Z7–14:OAc, but not Z8–14:OAc. *P. excessana* adults are usually warmly-coloured (and sometimes strikingly patterned) in contrast to the more sombre *P. avicenniae* and *P. octo*. The “*biguttana*” pattern (a diamond shaped white or cream patch in the forewing discal cell) is present in some individuals of all *Planotortrix* species.

Planotortrix avicenniae Dugdale, new species
(Fig. 7, 38, 49, 53, 66, 68)

[“*Planotortrix* Type M” of Foster et al. 1986: 156. “*Planotortrix* 1” “M” of Foster & Dugdale 1988: 229.]

escription. Adult colour pattern usually sombre, arcoal-brown with obscure pattern, sometimes ith pattern elements in ash or ochreous scales. ale costal fold: forewing length ratio 1:2.5–2.7, acus with expanded area longer than wide; socii in ateral view less than 1.5X as wide as gnathos arms (Fig. 53), vesica with 2 cornuti and basal lobe with obinations indistinct at $\times 32$ magnification (Fig. 8). Female cestum (Fig. 66) as in *P. excessana*.

calling pheromone major component: Z5–4:OAc (Foster et al. 1986).

arva. Head capsule, prothoracic shield, anal shield clerotised, contrasting with the grey-green faintly striped body and pallid setal pinnacula, forelegs arkened.

olotype ♂ : [BP] Matakana I Monro Block ex *vicennia officinalis* em. 11.5.61 [A. E. Marsack], n Type Collection NZAC.

Distribution. (Fig. 7). ND: Kerikeri Inlet (larvae); AK: Puhoi Estuary, Waitemata Harbour; WO: Piako estuary; CL: Firth of Thames, Kopu; Coromandel Harbour, Whangamata, Tairua estuary; BP: Tauranga Harbour, Matakana I.

Host. *Avicennia resinifera* (Verbenaceae)

Material examined. Holotype ♂, Allotype ♀, 2 ♂ ♂ 2 ♂ paratypes (same data as Holotype), 69 other specimens in NZAC.

Remarks. *P. avicenniae* males differ from those of other *excessana* complex species in the North Island in their (unusually) narrow socii and indistinctly scobinate basal lobe on the vesica. The costal fold: forewing length ratio overlaps with that of *P. octo*, and females are not consistently morphologically distinguishable from those of *excessana* and *octo*.

Although most members of an *avicenniae* population are typically charcoal or dull brown, others—particularly females—cannot be distinguished from sombre-coloured females of the other two species, both of which are parapatric as larvae, but are sympatric in flight range as adults with those of *avicenniae*.

The larva of *P. avicenniae* is distinctive, and with its brownish headcapsule, prothoracic and anal shield, darkened forelegs, and grey-green, faintly striped integument is quite dissimilar from the green-headed, green bodied larvae of *P. octo* and *P. excessana*.

The name is the genitive singular of *Avicennia*, the larval host.

Planotortrix flammea (Salmon)
(Fig. 8, 34, 73)

flammea Salmon, 1956: 575 (*Bactra*). Holotype ♂ Homer Forks FD, J. T. Salmon, NMNZ.

Diagnosis. Adult colour pattern purple-brown or orange-brown, hindwings and abdomen whitish ochreous, hindwings almost immaculate, and with a distinct purple or orange fringe. Male costal fold reduced (costal fold: forewing length 1:3.2–3.6); hindwing axillary cord tuft reduced, extending only halfway to hindwing anal angle; female cestum sclerotised laterally on each margin (Fig. 73).

♀ sex pheromone major components: Z5–14:OAc, Z7–14:OAc (ratio 50:50) S. P. Foster (pers. comm.).

Distribution (Fig. 8). GB, TO, TK, NN, BR, NC, MC, MK, FD, coastal to alpine.

Material examined. Holotype ♂ *flammea* NMNZ and 30 additional specimens (NZAC).

Host. *Leonohebe odora* complex, *Hebe salicifolia*, *H. stricta*, *H. subalpina* (Scrophulariaceae).

Remarks. *P. flammea* is now known from coastal *Hebe salicifolia* (Truman Track, Bullock Creek, BR), and from subalpine, frost flat, and alpine *Hebe* communities from Mt Hikurangi (GB) southwards. The type population (from Homer Basin, Upper Hollyford Valley FD) is more orange in overall colour, but no consistent morphological differences were seen. *P. flammea* adults resemble in general facies those of *P. notophaea* being somewhat slender, and males of both have conspicuously pallid antennae. The larvae are rarely found abundantly, in contrast to larvae of other *Leonohebe* and *Hebe*-feeding tortricines such as *Harmologa speciosa* Philpott, *H. sanguinea* Philpott, or *Pyrgotis consentiens* Meyrick.

Planotortrix notophaea (Turner)
(Fig. 35, 74)

notophaea Turner, 1926: 135 (*Tortrix*) Holotype ♂ Epping New South Wales (Australia), reared by A. Philpott, NZAC (ex ANIC).

distincta Salmon, 1948: 310 (*Ctenopseustis*, as subspecies of *obliquana*) Holotype ♂ Great Island, Three Kings Islands, AMNZ.

Diagnosis. Adults small (15–18 mm wingspan), often with forewing colour pattern arranged so that a diamond-shaped patch is present in the discal cell; male with a long costal fold (costal fold = forewing length ratio 1: 2.5–2.7), costal fold with “ceiling” sparsely clad in broad upright scales; hindwing anal pecten with stiff, strap-like, apically bifid scales; axillary cord tuft long, extending to hindwing anal

angle. Abdomen of both sexes with a lateral black stripe. Male uncus trowel-shaped, aedeagus with recurved apex, vesica with apical patch of broad spinules (Fig. 35) female cestum sclerotised along one margin only (Fig. 74).

♀ sex pheromone main component: Z7-14:OAc (Foster & Dugdale 1988: 229).

Larva. head capsule green with narrow brown or blackish stripes; body green (sometimes bright green), and with a more or less distinct white or cream lateral stripe; forelegs blackened.

Distribution. Three Kings Islands, ND-SI, coastal to montane forest.

Hosts. Polyphagous, more usually found on small-leaved, "hard-leaved" gymnosperms and dicotyledonous angiosperms.

Material examined. Holotype ♂ ♂ *notophaea* (NZAC ex ANIC), *distincta* (AMNZ), and 63 additional specimens (NZAC).

Remarks. *P. notophaea* is a rather slender, streamlined *Planotortrix*. Like *P. puffini*, and *Ctenopseustis* species, the axillary cord and epaulette tufts are composed of stiff long hair scales. Females of *P. notophaea* are distinctive in having the abdomen with a black lateral stripe (absent in sympatric *P. octo* and *P. excessana*). The larva is distinctive; no other known tortricine in New Zealand is bright green with black forelegs and a pallid to cream lateral stripe along the body.

In the absence of further records from Australia, I assume that the (adventive) type population at Epping, near Sydney, is now extinct.

Planotortrix octo Dugdale, new species (Fig. 6, 39, 47, 51, 72)

["*Planotortrix excessana* Type A" of Foster et al. 1986: 156, Foster & Dugdale 1988: 229; Foster & Roelofs 1988: 1-9.]

Description. Male costal fold: forewing length ratio 1:2.6-2.7, costal fold lacking broad scales on "ceiling". Male uncus (Fig. 47) with expanded portion distinctly longer than wide; socii as in Fig. 51, broad; vesica with basal lobe distinctly scobinate (viewed at $\times 32$ magnification), and 2 cornuti (northern populations) or 1 cornutus (southern populations), (Fig. 39).

Female genitalia. Cestum (Fig. 72) sclerotised over entire length, dextral margin with a shallow groove, widest posteriorly, in some specimens.

♀ sex pheromone major components: Z8-14:OAc, 14:OAc, (Galbreath et al. 1985; Foster et al. 1986: 156; Foster & Roelofs 1988: 7 in ratio 98:2; Foster & Dugdale 1988: 229).

Type material. Holotype ♂ "New Zealand MC Taitapu ex ivy, larvae coll. Sept. 1987 G. Burnip & J. S. Dugdale" NZAC.

Distribution (Fig. 6). ND-SL, coastal to timberline.

Hosts. polyphagous.

Material examined. Allotype ♀, 28 paratypes, same data as Holotype and 335 additional specimens.

Remarks. The name *octo* (8) refers to the major component of the female calling pheromone (Z8-14:OAc). *P. octo* is distinguished from *P. excessana* on male structures, and the different calling pheromone components. Galbreath et al. (1985) demonstrated the absence of cross-attraction between *P. octo* and *P. excessana*. Egg masses of *P. octo*, unlike those of *P. excessana*, are covered with a copiously applied whitish coating extending beyond the egg mass. Such whitish-coated egg masses have been observed in the field (W. P. Thomas, pers. comm.) and in laboratory colonies (D. Rodger, pers. comm.).

In *P. octo* the number of cornuti on the vesica is variable. In northern and western localities (ND-WN, NN-BR-WD in part) males usually have two cornuti on the vesica; in the southern group (NC, MC, CO), there is usually one cornutus.

Planotortrix octoides Dugdale, new species (Fig. 40, 48, 52, 56, 76)

Description. Medium-sized *Planotortrix*, wingspan 18-26 mm (both sexes); male forewing costal fold: forewing length ratio 1:2.9-3.5 (i.e., comparable with *P. excessana*). Socii width less than 1.5x width of gnathos arms (Fig. 52); male uncus expanded portion longer than wide, transtilla teeth congested (Fig. 48), more or less triseriate towards outer apex of each transtilla plate; aedeagal vesica basal lobe obscurely scobinate (at $\times 32$ magnification) (Fig. 40); female cestum (Fig. 76) expanded centrally, scarcely sclerotised and then only on the expanded portion. ♀ sex pheromone major component: Z8-14:OAc (Dr S. P. Foster, pers. comm.).

Larva. head capsule, prothoracic and anal shields sclerotised, ("brown-headed"); rest of body pale grey-green.

Type Material. Holotype ♂: "Chatham Islands NZ: Rangitira I. (South East I) 1-14 Dec. 1987 J. S.

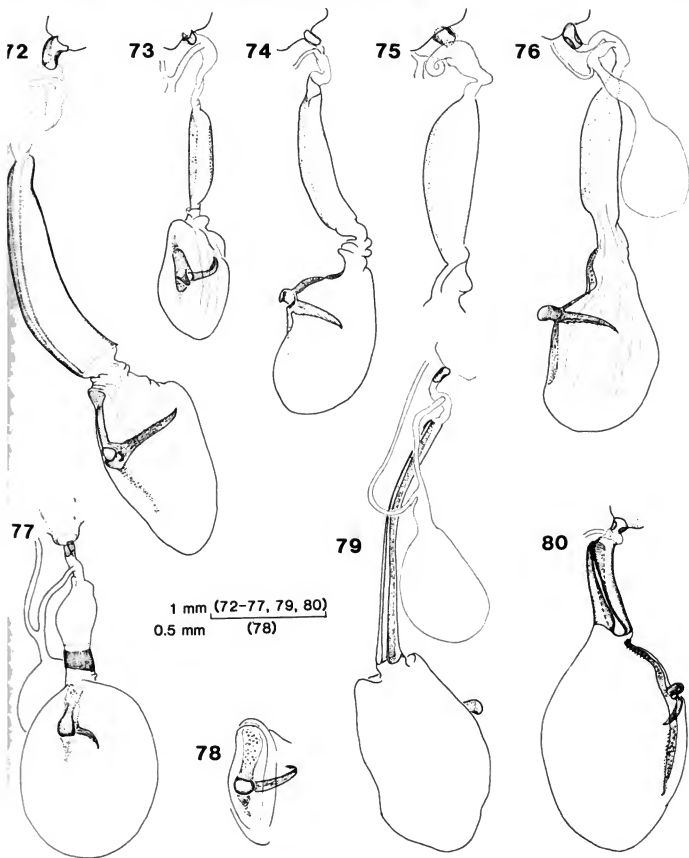


Fig. 72–80 *Planotortrix* and *Apoctena* species, female genitalia; 72, *Planotortrix octo*, Tai Tapu MC; 73, *P. flammea*, Ohakune Mountain Road TO; 74, *P. notophaea*, Golden Downs NN; 75, *P. puffini*, Lee Bay SI (corpus bursae omitted); 76, *P. octoides*, Rangatira I, Chatham I (male 1 single tip analysis); 77–80, *Apoctena* species, female genitalia; 77, *Apoctena conditana*, Nelson NN; 78, *A. orthopis*, ditto, signum; 79, *A. orthopis*, ditto, female genitalia; 80, *A. pictoriana*, Hanmer NC.

Dugdale". "L[ear]R[oller] coll. NM, ex *Mysine* em[erged] 6-8 Feb. 1988" NZAC.

Distribution. Chatham Islands: Chatham, Pitt, Rangitira (South East) Islands.

Hosts. polyphagous.

Material examined. "Allotype ♀ em. 14 Jan. 1988, STA [single tip analysis]", otherwise same data as Holotype, and 42 Paratypes, same data as Holotype and 26 additional specimens, variably patterned.

Remarks. The name *octoides* (similar to number 8, Latin) reflects the major component of the female calling pheromone, along with the morphological dissimilarity between this species and true *octo*.

As with *P. avicenniae*, *P. octoides* males have slender socii lobes (Fig. 52) and reduced scobinations on the basal lobe of the vesica (Fig. 40). The scarcely sclerotised ductus bursae (and then only on the middle third of the expanded portion of the ductus, (Fig. 76) distinguishes this species from *avicenniae* and the other members of the *excessana* complex.

P. octoides is an allopatric member of the *excessana* complex, and is endemic to the Chatham Islands, where it is the only *Planotortrix* species known. The host range includes both indigenous and introduced angiosperm trees and shrubs, including horticultural cultivars.

Planotortrix puffini Dugdale, new species

(Fig. 7, 36, 75)

[*Planotortrix* Type MBS of Foster et al. 1986: 156.

Planotortrix I "MBS" of Foster & Dugdale 1988: 229.]

Description. Medium sized to very large *Planotortrix*, wingspan 24-30 mm (males) and 26-40 mm (females). Male costal fold:forewing length ratio 1:2.5-2.7, costal fold "ceiling" with upright broad scales (as in *P. notophaea*); hindwing axillary cord tuft long and extending to hindwing anal margin, hindwing anal pecten composed of hair-like scales. Male uncus trowel-shaped (apically bluntly pointed), aedeagus apex acuminate, vesica lacking scobinations (Fig. 36). Female cestum expanded, widest posteriorly, sclerotised along one side of the expanded zone, as a single lateral strip (Fig. 75); some females with a more or less distinct, but broken blackened lateral stripe on abdomen.

♀ sex pheromone major components: Z5-14OAc, Z7-14:OAc in proportions (Z5:Z7:Z9) 3:97:2 (Foster & Dugdale 1988: 229).

Larva. Head, prothoracic and anal shields sclerotised, brown; rest of body grey or grey-green, forelegs often darkened.

Type Material. Holotype ♂: "NZSI Lee Bay, coastal. L[ear]R[oller] HI March 1987. J. S. Dugdale and S. J. Muggleston. Reared ex *Brachyglottis reinoldii* em[erged] 30 April 1987", NZAC.

Distribution (Fig. 7). FD: Breaksea I; SL: Nugget Point; SI: Mt Anglem, summit scrub; Lee Bay, Oban area, Ocean Beach, Port Adventure, Mason Bay (south end); Codfish I; Big South Cape I; coastal and subalpine.

Hosts. *Brachyglottis reinoldii*; *Celmisia lindsayi*, *Olearia colensoi colensoi*, *O. colensoi grandis*, *O. oporina* (Asteraceae).

Material examined. Allotype ♀ same data as Holotype, 63 Paratypes same data, and 76 additional specimens.

Remarks. *P. puffini* is a robust, usually large species with the slender (or "long-winged") facies of *P. notophaea*, which it closely resembles morphologically. Males may be distinguished from those of *P. notophaea* by the hair-like, rather than flattened, sword-like anal pecten scales, and females by the absence of, or weak development of a black lateral abdominal stripe (strongly evident in *P. notophaea*), as well as the broader forewings and more robust build. From the *excessana* complex, the long hindwing axillary cord tuft, the presence of broad scales on the costal fold "ceiling", the trowel-shaped uncus, and the narrowly laterally sclerotised cestum, serve to distinguish both *P. puffini* and *P. notophaea*.

P. puffini is so far known only from Nugget Point SL (on *Celmisia*), Breaksea Island FD, and Stewart Island and adjacent islands (on *Brachyglottis* and *Olearia*). Mr B. H. Patrick has reared it from summit *Olearia colensoi* on Mt Anglem, Stewart Island. I was unable to find *P. puffini*, or evidence of attack, on Chatham Islands, even though *Olearia oporina* var *chathamica* is present in extensive communities on the southern peaks of Rangitira Island.

The name *puffini* is the genitive singular (Latin) of *Puffinus* (the genus to which the muttonbird belongs. *P. puffini* is associated with "muttonbird scrub" (coastal *Olearia*, *Brachyglottis* species) over much of its range.

Apoctena Dugdale, new genus

[*Planotortrix* II] Foster & Dugdale 1988: 229, 231]

pe species. *Teras conditana* Walker, 1863.

agnosis. Medium to large, usually broadwinged
ricines; labial palpi porrect, usually over 1.8X
npound eye width. Male with a reduced costal
1 (ratio c. 1:4.0); costal fold lacking broad scales
“ceiling”, “floor” nude. Male hindwing (Fig. 18,
with a long, usually yellowish tuft of scales on
costal edge just beyond the frenulum, concealed
a series of acuminate scales either above or
ow, or both. Male genitalia (Fig. 41–44, 54); socii
ge (e.g., *flavescens*, Philpott 1928, fig. 68) or
derate (*conditana*, Fig. 54) or less than half gnathos
a length; uncus with a distinct neck, expanded
cal part oblong, or oval, or trowel shaped, or apic-
y or laterally emarginate; aedeagus orifice dorso-
tral (Fig. 41), dorso sinistral (Fig. 42) or apical
g. 43), vesica lacking a basal lobe and with 2–6
nuti, usually stout, sometimes ensiform (Fig. 41).

Female genitalia (Fig. 77–80: cestum usually
xter than corpus bursae (longer in *orthopsis*), either
erotised as a collar (most species, Fig. 77) or as a
x with a lateral longitudinal furrow along its
ire length (*orthopsis* (Fig. 79), *pictoriana* (Fig. 80),
num complete (Fig. 78).

Common female sex pheromone components:
1–14:OAc, Z11–14:OAc, and some species also
th Z9–14:OAc. (Foster & Dugdale 1988: 229).
cluded species (other nomenclatural details in
gdale 1988: 123, 125–126):

<i>octena conditana</i> (Walker, 1863)	n. comb.
<i>octena clarkei</i> (Philpott, 1930)	n. comb.
<i>octena fastigata</i> (Philpott, 1916)	n. comb.
<i>octena flavescens</i> (Butler, 1877)	n. comb.
<i>octena orthocopa</i> (Meyrick, 1924)	n. comb.
<i>octena orthopsis</i> (Meyrick, 1901)	n. comb.
<i>octena persecta</i> (Meyrick, 1941)	n. comb.
<i>octena pictoriana</i>	n. comb.
Felder & Rogenhofer, 1875)	
<i>octena spatiosa</i> (Philpott, 1923)	n. comb.
<i>octena syntona syntona</i>	n. comb.
Meyrick, 1909)	
<i>octena syntona laqueorum</i>	n. comb.
Dugdale, 1971)	
<i>octena taipana</i>	n. comb.
Felder & Rogenhofer, 1876)	
<i>octena tigris</i> (Philpott, 1914)	n. comb.
id one undescribed species known from males tly, Lochnagar Ridge, Paparoa Range BR.	

emarks. This endemic New Zealand genus is
stinguished by the presence of a tuft of modified
air-scales (Fig. 18, 19) on the costal edge of the
ale hindwing, near the frenulum.

Apoctena is not as homogeneous as *Planotortrix*
or *Ctenopseustis*. The aedeagus is variable in structure
particularly for orifice position (Fig. 41–44). The
female cestum states indicate three groups: *conditana*
et al. (Fig. 77), *orthopsis* (Fig. 79), and *pictoriana*
(Fig. 80). This grouping coincides with male
hindwing “pseudofrenular” states – the *conditana* et
al. state (Fig. 19), the *orthopsis* state (Fig. 18), and
the *pictoriana* state (the brush very long, extending
to at least one-third wing length, and exposed
dorsally). The present grouping under *Apoctena*
may be paraphyletic and needs closer analysis.

Apoctena species are largely broad-winged,
Planotortrix-like moths with the wings held flat-
folded in repose. The two narrow-winged species
are both characteristic of exposed (windswept) plant
communities – *A. persecta* (previously in *Epichorista*,
Dugdale 1988: 123) on *Coprosma* species, and *A.*
syntona syntona on the Auckland Islands largely on
Pleurophyllum (Asteraceae).

Not all the *Apoctena* species have been analysed
for female sex pheromones; of the five species
analysed, *A. orthopsis* is unusual (a) in having Z9–
14OAc in the pheromone (Foster & Dugdale 1988)
and (b) combining some *Ctenopseustis* and *Plano-*
tortrix notophaea morphological group characters.
The male of *A. orthopsis* has a well-developed axillary
cord tuft resembling that of *Ctenopseustis* species,
the scale sockets (Fig. 17) having the same 8-shape
configuration as the sockets of the expandable
Ctenopseustis axillary tuft (Fig. 15).

All *Apoctena* species have arboreal, or at least
above-ground feeding larvae. Some species are
polyphagous, (e.g., *A. conditana*, *A. syntona*, *A.*
flavescens), but six species (at least) are restricted to
a genus or family of host plants: *A. clarkei* on
Sücherus; *A. orthocopa* on *Cyathea*; *A. persecta* on
Coprosma; *A. pictoriana* on *Nothofagus*; *A. spatiosa*
on *Griselinia*. Larvae of *A. conditana*, *A. pictoriana*,
and *A. persecta* have a colour pattern, usually
consisting of a dark subdorsal stripe, and the dorsum
and lateral areas differentially tinted.

Six species are found in both North and South
Islands; two are restricted to the North Island (*A.*
orthocopa and *A. clarkei*, both on ferns), three are
known only from the South Island (*A. fastigata*, *A.*
persecta, and *A. taipana*). *A. syntona* is composed of
two polyphagous allopatric subantarctic populations:
A. s. syntona on Auckland Island and *A. s. laqueorum*
on the Snares.

Further work is needed on the suspected
synonymy of *spatiosa* with *taipana*, and on the status
of the synonyms of *conditana* as listed in Dugdale

(1988: 125). The morphological examination of *conditana* specimens for this paper included the Holotype (from Nelson), and Nelson-Marlborough Sounds specimens agreeing with the Holotype in colour pattern and structure. The name is derived from the Greek *apo* = away and *kteis*, *ktenos* = a comb; gender feminine, and draws attention to the apomorphic hindwing character.

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A genetic analysis of mallards, grey ducks, and their hybrids in New Zealand

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Abstract Variation at 39 allozyme loci in small samples of grey and mallard ducks from New Zealand showed no significant differentiation between populations and minimal heterozygosity (<0.010) in all populations. This finding is consistent with other observations of no allozyme differentiation among congeneric species of birds and with the conservative nature of allozyme divergence in birds generally. The data also suggest that both taxa have undergone genetic bottlenecks associated with their arrival in New Zealand.

Keywords *Anas superciliosa*; *Anas platyrhynchos*; grey duck; mallard duck; electrophoresis; populations; systematics; hybridisation; heterozygosity; genetic differentiation; allozymes

INTRODUCTION

The decline of the New Zealand grey duck (*Anas superciliosa superciliosa*), recorded with concern by several authors in the past 15 years (e.g., Caithness 1974), has been variously ascribed to habitat depletion and disturbance (Caithness 1982), competitive displacement by mallards (*A. platyrhynchos*) (Williams 1981), and genetic swamping by mallards (Delacour 1956; Gillespie 1985). In particular, the importance of hybridisation with the introduced mallard has been disputed (e.g., Williams & Roderick 1973, cf. Gillespie 1985; Haddon 1984). After undertaking captive breeding studies of the two species and their hybrids, Williams & Roderick (1973) proposed that both pre-zygotic and post-zygotic anti-hybridisation mechanisms were operating, and that hybridisation, if it did occur, would lead to grey duck genes entering the mallard gene pool rather than the reverse. Haddon (1984) disputed this view, arguing that Williams & Roderick's (1973) results were not statistically significant; however, he did not, as he claimed, demonstrate a complete absence of barriers to gene flow between the two duck species.

A parallel situation exists in North America where black ducks (*A. rubripes*) hybridise freely with mallards, and are declining, apparently as a direct result (Ankney et al. 1987). Ankney et al. (1986) quantified genetic differentiation among allopatric and sympatric populations of these two species. The mean genetic distances, D , between black duck populations (0.0007), between mallard populations (0.0010), and between mallard and black duck populations (0.0006) were very low; there was as much differentiation within the two species as between them. Ankney et al. (1986) concluded that their genetic data did not support even subspecific status for the black duck.

There are important differences in behaviour of the sympatric taxa in North America and New Zealand/Australia. Although the two American taxa differ in plumage and habitat use, there is no evidence for assortative mating (Brodsky & Weatherhead

1984). Female *A. rubripes* reared with conspecifics preferred conspecific males in choice experiments which did not allow male-male interactions, but preferred male mallards, which are socially dominant to those of their own species, in mixed-species male groups (Brodsky et al. 1988). In contrast, *A. superciliosa* both in Australia (Braithwaite & Miller 1975) and New Zealand appear to mate assortatively with reference to mallards. For example, counts of 2278 pairs in the Waikato district in 1967–68 comprised 1330 (58.4%) mallard pairs, 856 (37.5%) grey pairs, and only 92 (4%) hybrid pairings, the latter biased 18:1 in favour of mallard drake \times grey duck (unpublished Wildlife Service file data). Williams (1967) studied courtship of a mixed wild and pinioned population of grey ducks and mallards, and observed only one courting party in which mallard drakes displayed alongside grey drakes to grey females, and no examples of grey drakes joining a mallard courting party. T. A. Caithness (pers. comm.) has seen only one brief example of interspecies courtship among hundreds of observations at Pukepuke Lagoon; J. Dowding (pers. comm.) found that grey ducks formed a tight group within a large mixed aggregation of the two species on the Orewa sewage ponds during the shooting season.

Hybridisation may result from the behaviour, common in dabbling ducks (McKinney et al. 1983), of males forming groups once their mates are incubating and forced mating any unaccompanied females they encounter. Ankney et al. (1987) considered this to be the most important mode of hybridisation between mallards and black ducks; most replacement clutches may be fertilised in this way, regardless of the original mate choice before laying of the first clutch.

In situations where one species forms a very small proportion of a mixed population, hybrid pairings may be more common. Gillespie (1985), using morphological criteria, found that "pure" grey ducks, hybrids (including a range from very grey-like to very mallard-like), and "pure" mallards constituted 4.5%, 51.4%, and 44.1%, respectively of his total sample from Otago. He concluded that, "given the extremely low proportion of pure stock and the present levels of introgression, the mallard poses a threat to grey duck conservation in agricultural areas". He went on to state that no prezygotic or postzygotic antihybridisation mechanisms have developed between these two species. This view conflicts with many observations of the two species segregating in mixed populations.

We used allozyme electrophoresis to assess the degree of differentiation between grey ducks and mallards in New Zealand, and searched for suitable markers to assess the degree of introgressive hybridisation between them, as morphological methods have proved unable to distinguish hybrids after more than one generation of backcrossing to a parental species (Williams & Roderick 1973). Sample sizes are small because this was intended as a pilot study; had suitable marker alleles been found we would have analysed much larger samples.

METHODS

Sample collection

Tissue samples were collected from birds shot by hunters in late April/early May 1986. About 1 cm³ each of heart, liver, muscle, kidney, and pancreas were taken from each bird within an hour after death. Samples were stored in the field on solid CO₂ and placed in an ultrafreezer (–80°C) later the same day. Each bird was subjectively identified by morphological criteria to species or as a hybrid at the time of sampling, and the head was removed and frozen for subsequent confirmation of this identification by comparison with the relevant criteria of Gillespie (1985). Information on the origin, collection dates, and sizes of the samples used is given in Table 1.

The Pohangina grey ducks were collected from a single-species flock not associated with mallards or hybrids. The Manawatu mallard and hybrid samples were collected together and morphologically formed a continuously intergrading group; the division into two populations was an artificial one for the purposes of this study. There were no grey ducks in this population, except for one which passed through briefly and did not associate with other ducks. Grey ducks and mallards were collected together at Lake Onoke.

Table 1 Origins of samples used in this study.

Sample	Location	Date collected	No. of specimens
Manawatu mallard	Pukepuke Lagoon	1/5/86	4
Wairarapa mallard	Lake Onoke	1/5/86	3
	Mount Bruce	23/4/86	1
Manawatu hybrid	Pukepuke Lagoon	1/5/86	8
Wairarapa grey	Lake Onoke	1/5/86	1
Pohangina grey	Pohangina River	1/5/86	6

Electrophoresis

Electrophoretic techniques were those of Allendorf et al. (1977). Combinations of 4 tissue extracts, 4 buffer systems and 31 enzyme-specific stains, an eraser stain, and a general protein stain were screened for scorable activity, using a small number of representative specimens. Subsequently those combinations which showed clear discrete bands of enzyme activity were used to screen samples from available individuals. The observed patterns were assumed to represent Mendelian variation at genetic loci, with codominance of alleles. We labelled

enzymes, genetic loci, and alleles as recommended by Murphy & Crabtree (1985). Multiple loci encoding the same enzyme activity were numbered sequentially, beginning at the most cathodal, and alleles of polymorphic loci were identified by letter beginning at the most cathodal. Results were analysed using the BIOSYS-1 package (Swofford & Selander 1981).

RESULTS

Proteins encoded by 39 separate loci could be separated and scored consistently (Table 2). All

Table 2 Loci scored in this study, and the buffer conditions and tissues which allowed the clearest discrimination of each. H, heart; L, liver; Rw, Ridgeway buffer (Ridgeway et al. 1970); Ac, Amine-citrate buffer (Clayton & Tretiak 1972); Ph, Phosphate buffer (Selander et al. 1971); Pk, Poulik buffer (Selander et al. 1971).

E.C.N.	Enzyme/protein	Locus	Tissue	Buffer
1.1.1.1	Alcohol dehydrogenase	Adh-1	L	Ac
2.7.3.2	Creatine phosphokinase	Ck-1	L	Ph
		Ck-2	H	Ph
		Ck-3	L,H	Ph
3.1.1.1	Esterase	Es-1	L	Rw
		Es-2	L	Rw
1.2.1.12	Glyceraldehyde-phosphate dehydrogenase	Gapdh-1	L	Ph
		Gapdh-2	L	Ph
1.1.1.49	Glucose-6-phosphate dehydrogenase	Gd-1	L	Ph
		Gd-2	L	Ac
2.6.1.1	Glutamate-oxalacetate transaminase	Got-1	H,L	Ac
		Got-2	H,L	Ac
	General protein	Gp-1	L	Ac
		Gp-2	L	Ac
		Gp-3	L	Ac
		Gp-4	L	Ac
5.3.1.9	Glucose phosphate isomerase	Gpi-1	L	Ac
		Gpi-2	L	Ac
		Gpi-3	L	Ac
1.1.1.42	Isocitrate dehydrogenase	Icd-1	H,L	Ac
		Icd-2	L	Ac
1.1.1.27	Lactate dehydrogenase	Ldh-1	L	Ac
		Ldh-2	L	Ac
		Ldh-3	L,H	Ac
1.1.1.37	Malate dehydrogenase	Mdh-1	H	Ph
		Mdh-2	H,L	Ph
		Mdh-3	L	Ph
3.4.1.1	Peptidase	Pep-1	L	Rw
		Pep-2	L	Rw
		Pep-3	L	Rw
		Pep-4	L	Rw
		Pep-5	L	Rw
1.1.1.44	Phosphogluconate dehydrogenase	Pgd-1	L	Ph
2.7.5.1	Phosphoglucomutase	Pgm-1	L	Rw
		Pgm-2	L	Rw
		Pgm-3	L	Ac
1.1.1.14	Sorbitol dehydrogenase	Sordh-1	L	Pk
1.15.1.1	Superoxide dismutase	Sod-1	L,H	Ac,Ph,Pk
		Sod-2	L,H	Ac,Ph

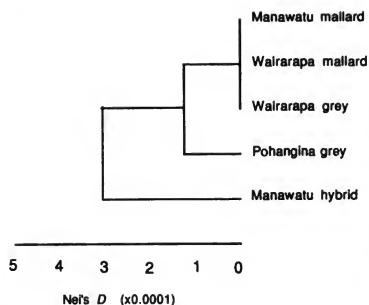


Fig. 1 Phenogram (UPGMA) of the five populations studied using Nei's (1978) D , generated by the BIOSYS package (Swofford & Selander 1981).

except two loci were monomorphic in all populations. Pgm-2 had three alleles and Pgm-3, two alleles. Neither polymorphic locus diagnostically separated the groups. Pgm-2b was common in all populations; Pgm-2a and Pgm-2c were found only as heterozygotes with Pgm-2b. Pgm-2a was found in two Pohangina greys and one Wairarapa mallard, and Pgm-2c in a single Manawatu mallard. Pgm-3a was fixed in both mallard and grey duck populations; Pgm-3b heterozygotes were seen in two Manawatu birds identified as hybrids, and no Pgm-3b homozygotes were found.

Heterozygosity within populations ranged from 0.000 in the single Wairarapa grey duck specimen to 0.009 in Pohangina greys (Table 3), and genetic distances between populations were very low (maximum distance—Nei's D —between groups in a cluster analysis = 0.00031, Fig. 1). A phenetic cluster analysis (Fig. 1) failed to separate the species.

DISCUSSION

Because of the combination of very low heterozygosity and absence of differences between the taxa, our genetic results add nothing further to understanding of the nature and extent of grey duck-mallard hybridisation, nor of its importance as cause of the decline of grey ducks in New Zealand. Had heterozygosity been high but differentiation absent, a panmictic hybrid swarm might have been inferred. On the other hand, allozyme differences that correlated with morphological differences between the taxa would have allowed assessment of the rate and direction of gene flow between them. Our study leaves uncorroborated the observations and conclusions of Gillespie's (1985) morphometric study, but does confirm the extremely close relationship of the two species.

These results are similar to those of Braithwaite & Miller (1975) who studied the same two species in southern Australia. They used cellulose-acetate, polyacrylamide, and gradient electrophoresis to study plasma protein variation, which was not amenable to Mendelian interpretation. Their results are therefore not directly comparable to ours, but like us they found no genetic method of identifying the species or their hybrids. They found a greater degree of variation within populations than we have, but again the measures are not directly comparable. Braithwaite & Miller (1975) concluded from their behavioural observations that there was little opportunity for gene flow between the species, a similar conclusion to that of Williams (1967) from his behavioural observations in New Zealand.

Ankney et al. (1986) in their study of genetic differentiation between mallards and black ducks (*A. rubripes*) in North America, found very small genetic distances between populations both within and between species, as we did. Like ours, the phenogram generated from their data failed to separate the two species.

Table 3 Heterozygosity measures for each population, calculated using the BIOSYS package (Swofford & Selander 1981). Loci are considered polymorphic if the most common allele has a frequency <0.99. Standard errors for heterozygosity equal the means in all populations.

Population	Sample size	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct count	Hardy-Weinberg
Manawatu mallard	4	1.0	2.6	0.006	0.006
Wairarapa mallard	4	1.0	2.6	0.006	0.006
Manawatu hybrid	8	1.0	2.6	0.006	0.006
Wairarapa grey	1	1.0	0.0	0.000	0.000
Pohangina grey	6	1.0	2.6	0.009	0.008

Patton & Avise (1986) compared a range of waterfowl taxa using starch gel electrophoresis. They recorded genetic distances (Nei's D) between species within genera of between 0.001 and 0.186. With these extreme values were found within *Anas*, the lowest value being that between *A. platyrhynchos* and *A. rubripes*. (This value is somewhat higher than those of Ankney et al. (1986) for the same taxa cause fewer non-variable loci were examined.) *A. nigripes* and *A. carolinensis* (= *A. crecca*) are also extremely closely related to these two species (exact genetic distances not supplied), differing only slightly in gene frequencies at polymorphic loci, despite *A. carolinensis* being morphologically quite distinct from, and sympatric with, the others. These distances are much lower than those between species in other waterfowl groups, confirming the molecular conservatism found in birds as a group. Further confirmation of this conservatism is found in studies of herring gulls (*Larus argentatus*), lesser black-backed gulls (*L. fuscus*), and great black-backed gulls (*L. marinus*) in Great Britain and Scandinavia. These species are also sympatrically without significant interbreeding, and the first two are connected by a circumpolar ring of intermediate forms. Allozyme electrophoresis (Tegelstrom et al. 1980; Rytman & Tegelstrom 1981) and immunoelectrophoresis (Rytman et al. 1980) failed to reveal any differences between species of geographic populations.

The black stilt (*Himantopus novaezealandiae*) and the parakeet (*Cyanoramphus auriceps forbesi*) are both subjects of management in New Zealand aimed at reducing a perceived conservation threat from hybridisation with more common congeners. Both have identifiable genetic differences from the hybridising species (Green 1988; Daugherty & Triggs unpubl. data), indicating that they are more differentiated from their relatives than the duck and all examples discussed above.

Both the mallard and grey ducks in our samples have lower levels of heterozygosity (Table 3) than those reported for the same species and most of their close relatives elsewhere. Patton & Avise (1986) reported heterozygosity levels of 0.037 for mallards, 0.028 for *A. rubripes*, and 0 for *A. fulvigula* (from a single individual, therefore not comparable). Parker et al. (1981) found $H=0.027$ in a wintering population of mallards. The levels of heterozygosity measured by Ankney et al. (1986) were greater; 0.047–0.076 for mallards and 0.047–0.059 for *A. rubripes*. These figures, 5–10× greater than ours, suggest that both species in New Zealand have been through genetic bottlenecks. Although our samples are small, this

difference is far too great to be solely caused by sampling bias, particularly given that the pattern is the same in all the New Zealand samples.

There were repeated releases of large numbers of mallards in New Zealand, initially (c. 1890–1920) of British stock mainly in Otago and Southland, and later (c. 1930–1960) of birds from the United States throughout the country (Caithness 1974). However, the birds released were bred in New Zealand from smaller initial introductions, and both the British and North American introductions were probably of game farm rather than truly wild stock; the American birds were probably at least partly originally derived from European game farms rather than wild North American birds (Braithwaite & Miller 1975). The populations therefore underwent a bottleneck on introduction to New Zealand on top of breeding in captivity, a situation which has been shown to lead to loss of genetic variability in many species (Schonewald-Cox et al. 1983). The grey duck is abundant in New Zealand subfossil deposits up to about 5000 years old, but records from older deposits are rare and of doubtful validity (P. Millener pers. comm.). We speculate that the low heterozygosity in the New Zealand grey duck population results from a founder effect; once the population was large the effect on gene frequencies of further rare immigrations would be negligible.

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Short Communication

Effect of temperature and photoperiod on pupal development rates in *Planotortrix octo* Dugdale* (Lepidoptera: Tortricidae)

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Abstract The pupal development rate of *Planotortrix octo* was monitored at 17 and 21°C at photophases of 0, 2, 6, 12, 14, 16, 18, and 24 h. Development rate was faster at 21°C and females developed significantly faster than males. A negative correlation between development rate and photophase was observed, with this being most marked at 7°C. Superimposed on this was a faster development rate at intermediate photophases (12–16 h).

This is discussed in relation to a possible circadian mechanism for control of both larval and pupal development.

Keywords Development; photoperiod; Lepidoptera; Tortricidae; *Planotortrix octo*

INTRODUCTION

Previous work on larval development rate in the indigenous tortricid *Planotortrix octo* (previously known as *P. excessana*) has shown a marked effect of photoperiod on duration and number of instars. Both of these are high during short days, with a sharp decline at long day photoperiods and a shallower decline in total darkness (Morris 1990a).

The pupal development rate was monitored at two temperatures under different photoperiods to determine whether a similar trend could be seen.

MATERIALS AND METHODS

Larvae were reared from first instars to pupation on general purpose diet (Singh 1983) at 17 and 21°C ± 1°C at photophases of 0, 2, 6, 12, 14, 16, 18, and 24 h. Instar number was determined from head capsule measurements. Since the disturbance caused by measuring may have had an effect on pupal development, a further group of insects were reared to pupation without disturbance. A detailed description of the insects and rearing procedure can be found in Morris (1990a, b).

Pupae were sexed and the number of days until eclosion was monitored.

Statistical analysis was performed on an IBM PC using the SAS package. All tests of significance were at $P < 0.05$.

RESULTS

Larvae developed through 5–7 instars, the number of instars having no effect on pupal duration. Disturbance also had no effect so results for disturbed and undisturbed pupae were pooled. Females developed significantly faster than males, and photoperiod also had a significant effect. There was a negative correlation between development rate and photophase, with this being most marked at 17°C.

The development rates at both temperatures are displayed on Fig. 1 and 2. Each point represents 29–61 insects.

DISCUSSION

From the Figures it appears as if photoperiod has two separate effects on development rate. Firstly, there is a direct negative correlation between photophase and development rate which suggests some aspects

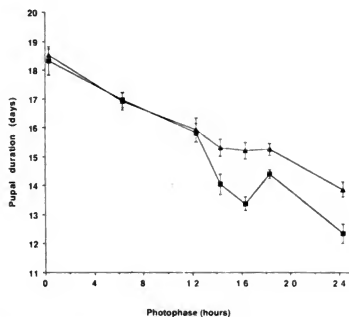


Fig. 1 Mean (\pm SEM) pupal development rate at 17°C. Squares = female; Triangles = male.

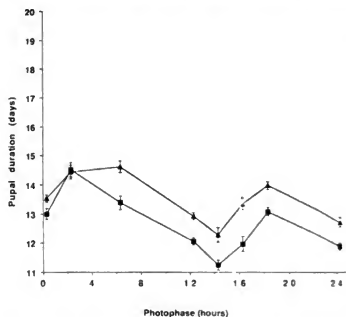


Fig. 2 Mean (\pm SEM) pupal development rate at 21°C. Symbols as for Fig. 1.

of metamorphosis are dependant on daylight. Similar correlations have been found for larval development rate in a number of Lepidoptera, but not for pupal development (Beck 1980; Danks 1987).

Secondly, there is a definite decline in development rate at photophases of 12–16 h at 21°C and 14–16 h at 17°C. The larval development rate shows a similar sharp decline at the same photophases at both temperatures (Morris 1990a, b) with a type 1 photoperiodic response curve typical of long day species (Beck 1980). A circadian mechanism for larval development has been suggested (Morris 1990a, b) based on the shape of the photoperiodic response curve. The response curve for pupal development shows a faster development rate at intermediate photophases, corresponding to a rarer type 4 photoperiodic response curve (Beck 1980). It also shows a longer critical photoperiod at the lower temperature and a slight decline in development rate in total darkness at the higher temperature. Both of these are characteristics of photoperiodic responses governed by a circadian mechanism (Beck 1980; Saunders 1982). A circadian mechanism could therefore be responsible for pupal development rate in *P. octo*.

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edatory and silk utilisation behaviour of *Gelotia* sp. indet. raneae: Salticidae: Spartaeinae), a web-invading gressive mimic from Sri Lanka

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Abstract An undescribed species of *Gelotia* was
found in the field in Sri Lanka and in the laboratory,
providing behavioural data for the first time for a
species from this spartaeine genus. Because the
Spartaeinae is regarded widely as a primitive
family of salticids, the results of this study are
discussed in relation to salticid evolution. During
social predation, *Gelotia*, like all spartaeines
described, often omitted elements which are usually
present in the predatory sequences of typical
salticids. It also, unlike most salticids, tended to
go at prey from close range rather than leap
from afar. *Gelotia* also invaded webs of other
spiders, practised aggressive mimicry by making
specialised vibratory signals, and ate the resident
spiders. Three other spartaeine genera, *Brettus*,
Cyba, and *Portia*, are the only other salticids known
to make vibratory aggressive mimicry signals.
Gelotia did not build a prey-catching web, although
other two spartaeine genera, *Portia* and *Spartaeus*,
are known to do so, but *Gelotia*, like *Portia*, hung up
a dead leaf on which to rest and oviposit.

Keywords spiders; Salticidae; Spartaeinae;
Gelotia; predation; aggressive mimicry

INTRODUCTION

Jumping spiders (Salticidae) are one of the major
animal groups in which acute vision has evolved,
but the evolutionary origins of these spiders and
their unique eyes remains poorly understood. Being
active diurnal spiders, salticids usually do not spin
webs or use silk in any way to capture prey, but
they do tend to build silk nests in which they moult,
oviposit, and sometimes mate and in which they
stay at night and during other periods of inactivity.
A few species make aberrant use of silk and the
behaviour of these species may provide clues about
salticid evolution.

The species in the recently revised (Wanless
1984) salticid subfamily Spartaeinae have a number
of morphological characters considered to be
plesiomorphic for salticids. Retinal ultrastructure
and behaviour of the studied species from seven
genera (*Brettus*, *Cocalus*, *Cyba*, *Phaeacius*, *Portia*,
Spartaeus, and *Yaginumanis*) in this subfamily have
been pivotal in recent discussions of salticid
evolution.

Retinal ultrastructure of spartaeines tends not to
be so highly organised as that of typical salticids, a
state which is most parsimoniously interpreted as
being primitive (Blest 1983, 1984, 1985; Blest &
Sigmund 1984; Blest et al. in press).

Portia is a genus of web-building and web-
invading spiders that make specialised vibratory
aggressive mimicry signals and eat other spiders
(Jackson & Blest 1982; Jackson & Hallas 1986a;
Forster & Murphy 1986). *Cyba* and *Brettus* are also
web-invading, but not web-building, spiders and
they practise aggressive mimicry and eat other
spiders (Jackson & Hallas 1986b; Jackson 1990a).
Cocalus invades webs and eats spiders, but does
not practise aggressive mimicry (Jackson 1990b).
Phaeacius is a specialised ambush predator which
neither builds nor invades webs (Jackson & Hallas
1986b; Jackson 1990c). *Spartaeus* is a web-building,
but not a web-invading, salticid. Although *Brettus*,
Cocalus, *Cyba*, and *Phaeacius* do not build webs,
they do build aberrant, web-like edifices, in which

to moult and oviposit, which contrast with the typical tightly woven tube-like nests typically built by salticids (Jackson 1979).

An initial study of *P. fimbriata* from Queensland led to a hypothesis about salticid evolution (Jackson & Blest 1982; also see Blest & Carter 1987) which includes speculations about the early steps in the evolution of the salticid visual system and behaviour. Comparative studies of salticids are crucial for making progress at trying to understand salticid evolution, especially additional information about spartaeines.

Spartaeines are primarily spiders of tropical Africa, Asia, and Australasia. Studying the behaviour of these spiders is difficult, not only because these tropical regions are remote for most arachnologists, but also because these spiders tend to be difficult to locate in the field. For most spartaeine species, it is probably unrealistic to expect long-term studies based on large numbers of spiders.

This paper is a study of the predatory and silk utilisation behaviour of a species from a previously unstudied spartaeine genus, *Gelotia*. *Gelotia* is evidently a rare spider. Only two specimens were available for this study, one found in 1986 and the other in 1987. Both were adult females and they were studied in the field and later taken to the laboratory.

MATERIALS AND METHODS

The species studied is an undescribed species of *Gelotia*, close to *G. syringopalpis* (F.R. Wanless, pers. comm.), which will be referred to simply as "*Gelotia*" (voucher specimens: British Museum of Natural History). Two adult females of this species were studied in nature (Sri Lanka) and the laboratory (Christchurch). The study site (Kaneliya) was rainforest and has been described elsewhere (Jackson & Hallas 1986a). Despite the extensive research that has been carried out on jumping spiders at this site, only these two specimens of *Gelotia* have turned up. Also, attempts to rear this species in the laboratory were unsuccessful. However, each of the two specimens available were observed extensively over a period of several months.

Spiders and insects with which *Gelotia* was tested and the types of tests for which each species was used are indicated in Appendix 1. Only adults of the insects were used, but the spiders were both juveniles and adults. All spiders and insects used as potential prey ranged from about the same to about half the size of the *Gelotia*.

More information about the insect and spider species used, maintenance and testing procedures terminology, and conventions for describing behaviours (e.g., definitions of phase and amplitude) are given elsewhere (Jackson & Hallas 1986a). Because *Gelotia*'s aggressive mimicry behaviour resembled aggressive mimicry behaviours of other spartaeines (Jackson & Hallas 1986a, b), the same terms are used and only brief descriptions are given here.

Gelotia is a moderately large (7–8 mm in body length), drab-coloured spider with sooty, orange-brown and pale white markings. It has large postero-medial eyes and, in general appearance, is somewhat similar to *Cocalus* (Jackson 1990b) except that *Cocalus*' carapace has a more raised profile.

OBSERVATIONS

Locomotion

If disturbed, *Gelotia* ran and leapt away, but normal locomotion was by steadily stepping more or less forward at moderate speed, often continuing for several seconds and covering 500–800 mm before stopping. The spider occasionally leapt accurately across gaps of as much as 100 mm in its path, but *Gelotia* usually walked around, instead of leaping across, obstacles in its path. When pausing after a bout of stepping, *Gelotia* occasionally pivoted about slowly, but it usually just remained motionless until it started walking about.

While walking and during pauses, *Gelotia* often waved its palps, legs, or both. Waving palps traced a circular path 1–2X per second. Palps moved up and in, passing in front of the chelicerae, to reach a maximum position where patellae were in front of antero-medial eyes. Next, without pausing, palps moved down and out alongside the chelicerae, then down and in so that tarsi were below the chelicerae as the next cycle began. Motion appeared smooth without evident pauses or changes of speed when palps changed directions. Bouts tended to last 2–10 s.

Legs I waved up and down (femoral motion), sometimes with a slight side-to-side motion superimposed (in and down, then up and out). Waving legs were held with joints flexed slightly and the two legs moved in either matching or alternating phase. Spiders often switched from matching to alternating phase, or vice versa, one or several times in a single bout of waving. Bouts of leg waving tended to last 2–10 s and legs moved at 1–2/s.



Fig. 1 *Gelotia* sp. female (facing up) walking on dead leaf suspended by guylines (guylines not visible in photograph).



Fig. 2 *Gelotia* sp. female leaving suspended leaf by walking up guyline.

Gelotia had no apparent difficulty walking on any type of web, and it did not stick to cribellate or cribellate glue. On densely woven webs, it simply walked as when not on a web, except that palp and leg waving was less pronounced and stepping was often especially slow. When on webs in which threads were spread apart, *Gelotia* made rotary probes (waved its forelegs about until catching thread) and slowly walked through the web.

When at rest, *Gelotia* adopted a posture not so different from its posture when walking.

Nesting and oviposition

When first seen in nature, each *Gelotia* was standing on a dead leaf suspended in a vacant web of another spider. Each web was a nonsticky inverted dome suspended between leaves and stems of trees in the rainforest. Apparently, these webs were built by

pholcids, several genera of pholcids being numerous in the study site.

The leaf on which *Gelotia* rested was suspended vertically 50–100 mm below the web dome. These leaves were dead, dry, and slightly concave. Each *Gelotia* had an egg-sac on the concave side of the leaf, and there were three or four heavy lines spun tightly across the concavity of the leaf and over the egg-sac. The leaves were in length about 3× the spider's body length and about 2× the spider's body width.

Some other salticids, *Portia* spp. and *Euryattus* sp. indet. (Jackson 1985a; Jackson & Hallas 1986a), are known to suspend dead leaves as resting and oviposition sites. When taken into captivity and kept in a large cage, each *Gelotia* female hoisted its leaf up on silk lines as has been described for *Portia* and *Euryattus*. Unlike *Portia*, *Gelotia* did not build a web around the leaf. Instead, like *Euryattus*,

Gelotia simply suspended its leaf by three or four guylines. Unlike the *Euryattus* guylines, however, *Gelotia*'s guylines were not especially heavy.

Each female made one additional egg-sac on a dead leaf given to it in the laboratory. To make an egg-sac, *Gelotia* spun a thick sheet of silk against the concave surface of the leaf, oviposited on the centre of the sheet, then covered the eggs with a second flimsier layer of silk. There were numerous white spots on the outer layer of silk. These spots were small tufts of very densely woven silk (1 mm or less in diameter) embedded in the structural silk of the egg-sac. Even without an egg-sac, *Gelotia* used a suspended leaf as a home base. The spider spent much of its time just resting on the leaf or walking about on the leaf (Fig. 1), sometimes watching insects that were moving about in the cage. The spider made intermittent forays away from the leaf by dropping down on a dragline or, usually, by walking up a guyline (Fig. 2). While away from the leaf, it stalked prey, then returned to the leaf by moving across a guyline. Prey was usually eaten away from the leaf, but *Gelotia* sometimes returned with its prey to the leaf, fed there, then dropped the prey.

Twice *Gelotia* was put in a large glass tank, with a vacant *Pholcus phalangiodes* web filling most of one side of the tank but with the other side being free of webbing. There were sticks scattered throughout the tank, and there were numerous dead

Fig. 3 *Gelotia* sp. female (facing down) on web of *Badumna longinquus* plucking with right palp and left leg I. This spider has lost left palp.



Fig. 4 *Gelotia* sp. female (almost head-on view) on web of *Badumna longinquus* plucking with right palp and left leg I. This spider has lost left palp.



ives on the bottom of the tank. On both occasions, *gelotia* suspended a dead leaf in the vacant *P. talangioides* web and used this leaf as its "nest" until removed about 1 week later.

Predation on insects away from webs

gelotia usually attacked prey by lunging on it from one range (generally from about half a body length away). During a lunge, the spider's body was propelled forward by rapid extension of the rear legs, but the legs did not leave the substrate. Occasionally, *Gelotia* made accurate leaps (i.e., all legs left the substrate) on actively moving flies, from as far as 50 mm away. Even with flies, however, *Gelotia* usually attempted to lunge instead of leap, although it only rarely got close enough before the fly moved away. *Gelotia* was more successful at catching moths, these insects not being so inclined to move away as *Gelotia* approached.

Predation on cursorial spiders

gelotia did not respond to nests of cursorial spiders, regardless of whether they were vacant or occupied, but it did respond to cursorial spiders away from nests in the same way that it responded to insects. *Gelotia* stalked and readily caught juvenile *Dolomedes minor* (Pisauridae) and *Clubiona cambridgei* (Clubionidae), especially once these spiders became quiescent, but rarely caught *Jacksonoides queenslandica* (Salticidae) because the salticids saw them coming and moved away.

Predation by invading alien webs

Gelotia readily invaded every type of web with which it was tested and caught the resident spider. Typically, *Gelotia* oriented toward the web, then approach it slowly, becoming steadily slower as it got closer. Usually *Gelotia* next moved very slowly onto the silk, remained inactive there for several minutes, then began to pluck with its palps.

Gelotia used three modes of plucking (up and down, forward and backward, and rotary forward and backward), each mode varying greatly over short time spans in specific characteristics (e.g., velocity and amplitude of movement). Palps moved more or less as the names suggest for each form of plucking (see Jackson & Hallas 1986a, b). The spider also switched frequently from one mode of plucking to another. Bouts of plucking were sometimes long and continuous (e.g., 10 min), but most lasted only 2–4 s and were followed by a

pause of variable length (often many minutes) before plucking was resumed.

One of the two *Gelotia* was missing a palp when collected (Fig. 3, 4). The other *Gelotia* was intact but, unfortunately, was not photographed palp plucking. The intact *Gelotia* sometimes plucked with just one palp at a time, but it usually plucked with both palps simultaneously. The same mode of plucking was usually adopted by the two palps, but amplitudes, velocities, and phasing of the two palps' movements often differed considerably. Often the two palps were not in matching positions on the web while plucking.

Although palp plucking was more common, *Gelotia* also occasionally plucked with legs I: one or both legs I forcefully pulled, pushed, or both on the silk one or several times, as has been described for *Portia* (Jackson & Hallas 1986a). *Gelotia* might palp and leg pluck simultaneously (Fig. 3, 4).

Sometimes *Gelotia* lured in the web spider. Once the web spider began approaching, *Gelotia*'s plucking became more stereotyped (i.e., *Gelotia* persevered with successful techniques). Lunging attacks were made when the web spider came to within a few millimetres of the signalling *Gelotia*.

When lunging, *Gelotia* brought its legs over the web spider then either stabbed (i.e., pierced the web spider's cuticle with its fangs then immediately withdrew) or grasped (i.e., held on) the web spider. Stabbed spiders ran away, then became paralysed. *Gelotia* watched the departing spider until paralysis set in, then approached and retrieved its victim.

Gelotia tended to remain at the edge of a web, plucking occasionally from here, but keeping at least legs IV on a non-silk substrate (e.g., a twig at the edge of the web). Sometimes it remained at the web edge for as long as 2–4 h. *Gelotia* might slowly move farther out on the web and advance slowly toward the web spider. *Gelotia* plucked intermittently as it advanced and eventually came to within a few millimetres of its victim and attacked by lunging.

There were two occasions when a *Gelotia* at the edge of a web leapt a few body lengths into a web to catch a web spider. Both times, the web spider had been quiescent for 10–40 min after *Gelotia* had lured it in. In one of these instances, *Gelotia* grasped and caught the web spider, but in the other instances *Gelotia* was deflected by intervening silk and the web spider escaped.

On four occasions, *Gelotia* entered a web and stalked a spider by slowly moving across the web, without plucking. When *Gelotia* got close it lunged

and caught the spider in three instances; in the other instance, *Gelotia* failed to get close and eventually left the web without plucking.

Gelotia sometimes stalked and lunged on insects that were caught in alien webs. In these instances, *Gelotia* simply walked across the web without making aggressive mimicry signals.

DISCUSSION

Egg-sacs

Gelotia's egg-sac most closely resembled *Portia*'s because both of these spartaeines put their egg-sacs on suspended dead leaves. However, all spartaeines studied make similar egg-sacs: eggs on a sheet of silk spun tightly against a rock, tree trunk or leaf and covered by a second silk sheet to partially conceal the eggs. The white "spots" in the second sheet of *Gelotia*'s egg-sac are also characteristic of the egg-sacs of spartaeine, but not of other, salticids.

Nesting behaviour

Gelotia did not build a typical, cocoon-like, salticid nest (see Jackson 1979). In fact, no spartaeine is known to build a nest like a typical salticid's. *Portia* and *Spartaeus* are the most unusual of the spartaeine salticids; they spin large prey-catching webs (Jackson & Hallas 1986a; Jackson & Pollard 1990). The other spartaeines studied rest under flimsy "web-like nests" spun on tree trunks, rocks, or green leaves. *Gelotia*'s brace threads over its egg-sac might be somewhat suggestive of these other spartaeines' nests.

Gelotia's "nest" is a hung up leaf. *Portia* also hangs up a leaf, but in its web. It is as though *Gelotia* hangs a leaf but does not bother with a web. Did the ancestors of *Gelotia* both build webs and hang up leaves, like *Portia*? This question is particularly intriguing because it has been suggested that all salticids had web-building ancestors and that some of *Portia*'s unusual behaviours are plesiomorphic within the Salticidae (Jackson & Blest 1982).

Euryattus is another salticid that, like *Gelotia*, hangs up a dead leaf without spinning a web to surround the leaf (Jackson 1985). *Euryattus* is not a spartaeine, but it has morphological characteristics that may be plesiomorphic (Blest 1987). *Euryattus*' biology is suggestive of web-building ancestry. Only large juveniles and adult females of *Euryattus* hang up leaves, but small juveniles do not spin typical cocoon-like nests. Instead, small juveniles of *Euryattus* spin webs!

Gelotia juveniles have not been studied yet. However, *Gelotia* adults do have an affinity for webs. Instead of spinning their own web, they appear to prefer to put their leaves in other spiders' webs.

Predatory behaviour

There are some other remarkable similarities between *Gelotia* and *Portia*. Both are web-invading araneophages. Both make vibratory aggressive mimicry signals and both have the ability not to adhere to sticky webs. No non-spartaeine salticids are known to have these two characteristics. There are other spartaeines with these characteristics, however. *Brettus* and *Cyrra* are aggressive mimics and do not adhere to sticky webs (Jackson & Hallas 1986b; Jackson 1990a). *Cocalus* invades webs and does not adhere to sticky webs, but it is not an aggressive mimic (Jackson in 1990b).

In some details of its web-invasion behaviour, *Gelotia* is more like *Brettus*, *Cocalus*, and *Cyrra* than like *Portia*: *Gelotia*, like *Brettus*, *Cocalus*, and *Cyrra*, tends to remain mostly at the edge of the alien web, whereas *Portia* frequently goes completely into the alien web. *Gelotia*, also like *Brettus*, *Cocalus*, and *Cyrra*, appears to put greater emphasis on cursorial predation than *Portia* does. *Gelotia*, *Brettus*, *Cocalus*, and *Cyrra* readily pursue insects outside of webs, whereas *Portia* does not. Also, *Portia*, unlike the other four web-invading spartaeines, spends most of its time in webs whether they be its own or alien. Even when being cursorial predators of insects, however, no spartaeines studied are really "typical" salticids.

Predation

The typical responses of visually hunting salticids to their prey (active insects) has been analysed in detail by Forster (1977). The cursorial predation sequences of all spartaeines studied are "incomplete" in comparison to the sequences Forster described.

Perhaps spartaeine ancestors were like typical salticids and perhaps spartaeine cursorial predatory behaviour is a modification (or degeneration) of "typical" cursorial predatory behaviour. Alternatively, the spartaeine style of cursorial predation, along with some of the other behaviours of these spiders, may be plesiomorphic for salticids.

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APPENDIX 1

Spiders and insects used as potential prey or as sources of eggs, webs, and nests in tests with *Gelotia* listed alphabetically by species. Information will be given in the following order: species, family (plus order for insects), collection site, description, types of tests. CS: spins cribellate sticky web. CU: non-salticid cursorial spider. ES: ecribellate sticky web. F: *Gelotia* put into cage with spider or insect, or spider or insect put in cage with *Gelotia*; cage free of nests and webs. I: insect; all others,

spiders. NE: eggs in vacant nest of cursorial spider. NO: nest occupied by cursorial spider, but no eggs present. NS: non-sticky web. SS: social species; builds communal web. TS: typical cursorial salticid. WB: web-building spider. WE: eggs in vacant web. WO: web occupied by host spider. WI: insect in vacant web of *Stegodyphus sarasinorum*. WV: vacant web with no eggs.

Achaearanea sp. 1. Theridiidae. New Zealand. WB, ES, WE, WO.

Araneus pustulosus Araneidae. New Zealand. WB, ES, WO.

Badumna longinquus (L. Koch). Amaurobiidae. New Zealand. WB, CS, WO.

Cambridgea antipodiana (White). Stiphidiidae. New Zealand. WB, NS, WO.

Chelaner antarctica. Hymenoptera, Formicidae. I, F.

Clubiona cambridgei L. Koch. Clubionidae. New Zealand. CU, F, NE, NO.

Ctenopseustis sp. Lepidoptera, Tortricidae. New Zealand. I, F, WI.

Dolomedes minor L. Koch. Pisauridae. New Zealand. CU, F.

Drosophila immigrans. Diptera, Drosophilidae. Culture. I, F, WI.

Drosophila melanogaster (Meigen). Drosophilidae. Culture. I, F, WI.

Inola subtilis Davies. Pisauridae. Australia. WB, NS, WO.

Jacksonoides queenslandica Wanless. Salticidae. Australia. TS, F.

Melancha sp. 1. Lepidoptera, Noctuidae. New Zealand. I, F.

Musca domestica (L.) Diptera, Muscidae. Culture. I, F, WI.

Predatory and nesting behaviour of *Cocalus gibbosus*, a spartaeine jumping spider (Araneae: Salticidae) from Queensland

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Abstract *Cocalus gibbosus* was studied in the field in Queensland and in the laboratory. This is the first behavioural study of a species from the spartaeine genus *Cocalus*. *C. gibbosus* often omitted elements which are usually present in the predatory sequences of typical salticids and tended to lunge at prey from close range rather than leap from afar. Experiments showed that *C. gibbosus* prefers moths to other prey. In nature, *C. gibbosus* moulted and oviposited on silk sheets spun against tree trunks, and in the laboratory on sides of cages or blocks of wood, but this species never built an enclosing nest like typical salticids nor a large prey-catching web like some other spartaeines. *C. gibbosus* stalked across alien webs to catch spiders and insects, but it did not make vibratory signals. It did not stick to cribellate or ecribellate glue on alien webs. The behaviour of *C. gibbosus* is compared to that of other spartaeine salticids.

Keywords Spiders; Salticidae; Spartaeinae; *Cocalus gibbosus*; predation; behaviour

INTRODUCTION

Salticids have acute vision and unique, complex eyes (Blest 1985; Land 1985). Not surprisingly, these spiders tend to be active diurnal hunters that

do not spin webs or use silk in any way to capture prey. Their use of silk tends to be restricted to laying down draglines and building cocoon-like nests in which they moult, oviposit, and sometimes mate and in which they stay at night and during other inactive periods.

Comparative studies of spartaeines have been pivotal in recent discussions of salticid evolution (e.g., Jackson 1986). Spartaeines are unusual salticids (Wanless 1984). All studied spartaeines make aberrant use of silk and two genera (*Portia* and *Spartaeus*) spin large prey-catching webs (Jackson & Blest 1982; Jackson & Hallas 1986a; Jackson & Pollard 1990). Also, spartaeines tend to have retinal ultrastructure that is less highly-organised (and less derived) than that of typical salticids (Blest 1985, unpubl. data; Blest & Carter 1987, 1988; Blest et al. in press).

Spartaeines are primarily spiders of tropical Africa, Asia, and Australia (Wanless 1984). Studying the behaviour of these spiders is difficult, not only because these tropical regions are remote for most arachnologists, but also because many of these spiders are difficult, if not impossible, to collect in large numbers. For most spartaeine species, it is probably unrealistic to expect long-term studies based on large numbers of spiders.

This paper is about the predatory and nesting behaviour of *Cocalus gibbosus* Wanless, a member of a previously unstudied spartaeine genus. This spider appears to be rare. Only five specimens were found in nature during a 7-year period.

There are four species in this genus: *C. concolor* Koch, *C. limbatus* Thorell, *C. murinus* Simon, and *C. gibbosus*. *C. gibbosus* is known only from Queensland, Australia, only a single specimen (an adult male) being on record before this study. The other species are Indonesian (Wanless 1981).

MATERIALS AND METHODS

Field work was based on five specimens: one found in 1982 (December, adult female); two in 1987



Fig. 1 *Cocalus gibbosus* female viewed head-on. Note raised profile. Antero-medial, antero-lateral, and postero-medial eyes in view.



Fig. 2 *Cocalus gibbosus* female. Viewed from side. Note raised profile of carapace. Antero-medial, antero-lateral, and postero-medial eyes clearly in view. Left postero-lateral eye on rearward incline of carapace and does not show up well.

(May, one adult and one subadult female); and two in 1989 (December, one subadult female and one subadult male). The study site was rainforest and has been described previously (Jackson & Hallas 1986a).

Each field specimen was also studied in the laboratory, and additional specimens were obtained by rearing offspring in the laboratory. Spiders and insects with which *C. gibbosus* was tested, and the types of tests for which each species was used, are shown in Appendix 1. These spiders and insects ranged from about the same to about half the size of the *C. gibbosus*. Only adults of the insects were used, but the spiders were both juveniles and adults. More information about the insect and spider species used, maintenance and testing procedures, terminology, and conventions for describing behaviours are given elsewhere (Jackson & Hallas 1986a).

C. gibbosus is a medium-sized salticid, adult body lengths being 7–9 mm. It has dull orange, brown, grey, and white markings which render the spider cryptic on tree trunks in the rainforest. Males and females are not very different in size and markings. The *C. gibbosus* carapace has a moderately raised profile and posterior medial eyes are large, as in most spartaeines (Fig. 1, 2).

In nature, all *C. gibbosus* were found on tree trunks. In the laboratory, these spiders were kept in glass tanks or large plastic boxes with wooden boards on the floor, as noted before, to simulate tree trunks (see Jackson & Hallas 1986a).

In casual observations, *C. gibbosus* seemed to catch moths more readily than it caught more active prey. A formal testing procedure was set up in an attempt to confirm this. A single housefly or a single noctuid moth was put in a cage with the spider at 0900 h (laboratory photoperiod was 12L:12D, lights on at 0800 h) and left for 24 h. The cage was checked periodically during the day. Checks were frequent enough so that, in most instances, if prey was captured, *C. gibbosus* was seen feeding. When, occasionally, *C. gibbosus* completed feeding between checks, it was obvious from the masticated remains that *C. gibbosus* had eaten the prey.

All tests were carried out using prey about one-half to three-quarters the size of the spider. The spiders were laboratory-reared large juveniles and adults. Two tests were carried out in random order on successive days with each individual *C. gibbosus*: one test with fly and one test with moth. No individual *C. gibbosus* was tested more than once while it was in any given instar, but each spider was tested again if it moulted. Data from the same spider in different instars were treated as independent.

OBSERVATIONS

Oviposition and nesting

Cocalus gibbosus never built an enclosing nest. Most of the time it had no silk structure at all, but



Fig. 3 *Cocalus gibbosus* female (viewed from front) standing over egg-sac built in open (no nest). Note numerous white "spots" on silk of egg-sac.



Fig. 4 *Cocalus gibbosus* female (viewed from above) facing down while standing over egg-sac in open (no nest). Note numerous white "spots" on silk of egg-sac.

simply spent periods of rest (e.g., at night) motionless on the side of the cage or on the wood put in the cage. However, juveniles always before moulting, and females sometimes before ovipositing, built flimsy arrays of silk over slight indentations either on the surfaces of cages or the wood in their cages. These arrays ("nests") were about 2–3 × the spider's body length in diameter.

Spiders stood on the substrate under their nests and juveniles moulted while standing under the silk. There was little silk spun against the substrate under the nests of juveniles.

Females spun their egg-sacs on the substrate either under a nest or out in the open (Fig. 3, 4). To make an egg-sac, *C. gibbosus* spun a thick sheet of silk against a block of wood or the side of a cage, then oviposited on the centre of the sheet and covered the eggs with a second flimsier layer of silk. When the egg-sac was under a nest, it had a diameter slightly less than that of the nest, and it was positioned directly under the nest. Regardless of whether she had a nest, a female usually stood centred over her eggs with her legs on the silk of the egg-sac. *C. gibbosus'* egg-sac was always covered by white "spots". These spots were small tufts of very densely woven silk (1 mm or less in diameter) embedded in the structural silk of the egg-sac (Fig. 3, 4).

Each adult *C. gibbosus* female found in nature was in a nest standing over an egg-sac on a tree

trunk. The subadults found in nature, were simply standing or walking on the tree trunks.

Locomotion

If disturbed, *C. gibbosus* ran and leapt away, but normal locomotion was by slow, more or less steady stepping. The spider often continued stepping for many seconds and covered 300–500 mm before pausing. Occasionally, the *C. gibbosus* crossed over gaps in its path by making accurate leaps of as much as 80 mm, but leaping was not a regular part of this spider's locomotion. Usually, *C. gibbosus* walked around, rather than leaping over, obstacles in its path.

When *C. gibbosus* paused after a bout of stepping, it occasionally pivoted slowly about. Usually, however, *C. gibbosus* just remained motionless until starting to step again. *C. gibbosus* often kept its palps motionless while walking, but sometimes waved them up and out then down and in while stepping and just before starting to step after a pause. The two palps moved in matching phase at 1–2/s.

Cocalus gibbosus often used all legs while stepping, but sometimes waved legs I and II while stepping. It only rarely waved legs during pauses between stepping bouts. Generally, the two legs I moved simultaneously in matching phase with one or both legs II also moving simultaneously, but



Fig. 5 *Cocalus gibbosus* female feeding on moth. Viewed from above. Spider facing down.

often lagging slightly behind legs I. Waving legs moved up and somewhat out then down and somewhat in at 1–2/s. Movement was primarily femoral.

Cocalus gibbosus had no apparent difficulty walking on any type of web, and it stuck to neither cribellate nor ecribellate glue. On densely woven webs, *C. gibbosus* simply walked the same as it walked when not on a web, except that palp and leg waving were rare and stepping was often especially slow. When on webs in which threads were more spread apart, *C. gibbosus* made rotary probes (waved forelegs about until catching a thread; see Jackson & Blest 1982) and slowly moved about through the web.

When at rest, *C. gibbosus* adopted a posture not noticeably different from its posture when walking. *C. gibbosus* generally faced down when resting on a vertical surface.

Predation on insects away from webs

Cocalus gibbosus usually attacked its prey by lunging on it from close range (generally from about a half body length away). During a lunge the spider's body was propelled forward by rapid extension of rear legs, but legs did not leave the substrate. When leaping, all legs left the substrate. *C. gibbosus* occasionally made accurate leaps from as far away as 50 mm to catch an actively moving fly. Even with flies, however, *C. gibbosus* usually attempted to lunge instead of leap. Yet, attempts to catch flies by lunging were rarely successful. Moths, in contrast, were readily captured by lunging.

In a typical predatory sequence ending with lunging, *C. gibbosus* approached its prey slowly, initially with little or no palp and leg waving. If the spider got to within 20–50 mm without the prey moving away, forward motion became exceedingly slow, sometimes almost imperceptible. Moths were the only insects tested that routinely remained motionless long enough for *C. gibbosus* to get this close (Fig. 5).

When close to the prey, *C. gibbosus* usually began waving legs, but only intermittently and slowly (c. 1/s). Also, unlike leg waving during normal locomotion, *C. gibbosus* now tended to wave one leg at a time (usually, but not always, a leg I), or it might wave legs I and II on one side with the opposite legs I and II remaining stationary. The spider tended to wave the leg (or, sometimes, two legs) on one side 2–4 times, then wave the leg (or two legs) on the other side 2–4 times, continuing to ease forward toward the prey as it did so.

The spider's progress toward the prey was often exceedingly slow. The spider might, for example, ease forward then pause for several minutes, wave a leg I on one side, pause for several more minutes, wave the opposite leg I, pause again for several minutes, ease forward again, and so forth.

When the spider got to within a few millimetres of the prey, it might stand for several seconds (or even minutes) before lunging at it. As the spider got progressively closer, it brought its forelegs more and more forward, so that eventually (usually by the time the spider was within c. 20 mm of the prey) tarsi I and II were in front of the spider's chelicerae.

Sometimes the spider touched the prey with its waving legs then lunged as the prey began to move. If the prey did not move, the spider might pause for several seconds or minutes then wave a leg and touch the prey again, or it might simply lunge without waving again.

While easing toward the prey, the spider performed intermittent, slow, slight rocking motions c. 1–2/s, c. 2 mm). These motions were primarily forward then backward, with a slight up and down movement superimposed (up when going forward, down when going backward). The rocking spider's body moved smoothly without pausing. There were usually 2–4 cycles of rocking in a bout, after which the spider either paused or continued to advance slowly.

The rocking spider never waved but instead kept all legs on the substrate. Sometimes the spider began rocking as soon as it started walking after a pause, or it might start walking then begin to rock as it walked. Rocking was performed primarily when the spider was within a few centimetres of the prey and moving very slowly, and the spider sometimes rocked right up to the moment of lunging at the prey.

In formal tests, *C. gibbosus* captured moths more frequently than flies. There were 22 test pairs. In 12, *C. gibbosus* ate the moth but not the fly; *C. gibbosus* ate the fly but not the moth in only 3 (McNemar test for significance of changes, $P < 0.05$). *C. gibbosus* ate both the moth and the fly in three test pairs and ate neither in four.

Predation on cursorial spiders

Coccalus gibbosus did not respond to nests of cursorial spiders, regardless of whether they were vacant or occupied, but *C. gibbosus* did respond to cursorial spiders away from nests in the same way that it responded to insects. *C. gibbosus* stalked and readily captured *Dolomedes* and *Clubiona* but rarely captured salticids because the salticids saw them coming and moved away.

Predation on insects that landed on nests

Fruit flies that landed on nests were sometimes restrained briefly by the silk. On seven occasions, a female in her nest came out of the nest then walked slowly across the nest toward the fruit fly. On two of these occasions, the spider lunged and caught the fruit fly, but the fly escaped before the spider reached it in the other instances. On another 16 occasions (4, adult females; 12, juveniles), fruit flies that became entangled on the nest of a *C. gibbosus* were ignored by the spider.

Predation by invading alien webs

Coccalus gibbosus was never seen to leap into alien webs to catch spiders or insects, nor was any

aggressive mimicry seen, but *C. gibbosus* did sometimes stalk across sheet and orb webs and catch the resident spider or an insect. *C. gibbosus* advanced very slowly, sometimes rocking and waving when close, and lunged to attack the spider or insect, as during predation away from webs. Generally, *C. gibbosus* did not go very far into the web but, instead, remained at the edge, sometimes remaining there for many hours; *C. gibbosus* attacked web spiders that eventually came close to the web edge.

DISCUSSION

Crypsis and rest postures

When at rest, *C. gibbosus* adopted a posture not so different from its posture when walking, as is probably generally true of salticids. This contrasted, however, with *Portia* and *Brettus* (Jackson & Hallas 1986a, b), two spartacines which adopt a special cryptic rest posture with legs and palps pulled in close to the body. *Portia*'s and *Brettus*' rest postures are apparently related to special protective resemblance to detritus. *C. gibbosus* seems to be eucryptic (see Robinson 1969) on tree trunks, a special posture like *Portia*'s and *Brettus*' not seeming relevant to eucrypsis. *Portia* is morphologically a highly cryptic spider and resembles detritus in a web when in its special rest posture. *Brettus* at rest resembles detritus on a leaf. Another spartacine, *Phaeacius*, lives on tree trunks and is highly eucryptic (Jackson & Hallas 1986b). Resting *Phaeacius* adopt a special posture in which they flatten their bodies against a tree trunk. *Phaeacius*, unlike *C. gibbosus*, is primarily an ambushing predator. Perhaps the adoption of a special posture by *Phaeacius* but not *C. gibbosus* is related to differences in these spiders' predatory behaviour (Jackson 1990c).

Locomotion

The leg waving of *C. gibbosus* waving was somewhat similar to that of another spartacine, *Cyrba* (Jackson & Hallas 1986b; Jackson 1990a). The waving style of *Cyrba* has been called "swim waving" because of the pronounced out-and-in motion superimposed on the up-and-down motion. *C. gibbosus* moves its forelegs in basically the same way, except that the legs of *C. gibbosus* do not appear so much as though they are "swimming" because the out-and-in motion is not so pronounced.

Both *C. gibbosus* and *Cyrra* wave legs I and II simultaneously, with legs II tending to lag behind legs I. Many non-spartaeine salticids wave legs I when walking and during pauses between bouts of walking. Waving legs I and II together is an unusual characteristic of *C. gibbosus* and *Cyrra*. Other spartaeines, especially *Portia* (Jackson & Blest 1982), wave legs other than legs I, but in less regular fashion.

Nests and webs

Is the flimsy silk array under which *C. gibbosus* rested, moulted and placed its egg sac a "web" or a "nest". The terms "web" and "nest" are normally left undefined in discussions about spiders and there is probably little point in dwelling on definitions. What is clear is that *C. gibbosus* builds something that is more open than the typical cocoon-like nests of most salticids (Jackson 1979), and *C. gibbosus* may make some use of this silk array when catching prey.

The design of webs vary greatly among spiders and the ways in which webs assist spiders in prey-capture are often complex and variable. Emphasis on the trapping function of webs can be misleading. Although some webs thoroughly ensnare certain types of prey, the webs of many species normally detain prey only briefly. Often, to say that the prey's locomotion has been impaired by the web is more accurate than saying that the prey has been trapped. For the webs of some species, other functions such as prey-detection may be more important than prey-trapping (Witt 1975). Many species spin small, simple structures that have functions in prey-capture similar to large webs. Even when these structures consist of only a few threads, or even a single thread, they are frequently referred to as "webs" (Lubin 1986).

What *C. gibbosus* builds might be described as a rudimentary web or a web-like nest. It might also be envisaged as a degenerate nest if *C. gibbosus*' ancestors built cocoon-like nests. Alternatively, it might be envisaged as a degenerate web if *C. gibbosus*' ancestors built large prey-capture webs.

Comparative information about other spartaeines and other primitive salticids appears to give stronger support to the latter possibility—that *C. gibbosus* builds a degenerate web instead of a degenerate nest. No spartaeines are known to build cocoon-like, densely woven nests. *Brettus*, *Cyrra*, and *Phaeacius* make silk arrays very similar to that of *C. gibbosus* (Jackson & Hallas 1986b; Jackson 1990a, c), and *Portia* and *Spartaeus* make large prey-catching arrays which are unequivocally

"webs" (Jackson & Hallas 1986a; Jackson & Pollard 1990). Lyssomaninae is another subfamily of salticids that is widely regarded as "primitive" (Wanless 1980). These spiders also build web-like nests (Hallas & Jackson 1986; Jackson 1990b) with similarities to the web-like nests of *C. gibbosus*, *Brettus*, *Cyrra*, and *Phaeacius*; no lyssomanines are known to build enclosing nests of the type typical of advanced salticids.

Egg-sacs

The egg-sac of *C. gibbosus*, with its characteristic white "spots", was remarkably similar to egg-sacs of *Brettus*, *Cyrra*, *Gelotia*, *Phaeacius*, and *Portia* (Jackson & Hallas 1986a, b; Jackson in 1990c, d), all of which are covered with similar white "spots". *C. gibbosus* differed from the other spartaeines by putting an especially large number of "spots" on its egg-sac and by generally spinning a denser sheet of silk over the eggs. Eggs thus tended to be less conspicuous under the silk of *C. gibbosus* egg-sac than under the silk of the other spartaeines egg-sacs. The denser covering *C. gibbosus* puts over its egg-sac may be related to this spider's tendency to leave its egg-sac in the open.

Predation

Salticids are typically cursorial predators of active insects. Forster (1977) analysed typical salticid hunting sequences. The first phase, "orientation", consists of three distinct stages: "alert", "swivel" (cephalothorax pivoted so that the principal eyes face the prey), and "align" (abdomen moved into alignment with the cephalothorax). In the next phase, "pursuit", there are three alternatives: "walk", "run" (prey rapidly chased), and "stalk" (salticid slowly advances toward the prey). The final phase, "attack-capture", has three stages: "precrouch" (a pause), "crouch" (body pressed close to the substrate), and "jump" (by extending legs III and IV, the spider is propelled onto the prey).

The predatory sequences of *C. gibbosus* and all spartaeines studied almost never fully correspond to this description for typical salticid predation. Instead, spartaeine sequences tend to be "incomplete" when compared to the "typical" sequence. Spartaeines tend just to walk toward their prey. Also, spartaeines normally lunge instead of leap on their prey.

Phaeacius and *Spartaeus* are, like *C. gibbosus*, spartaeines that live on tree trunks and, like *C. gibbosus*, feed especially on moths (Jackson &

Hallas 1986b; Jackson & Pollard 1990; Jackson 1990c). *Phaeacius* differs from *C. gibbosus* by being primarily an ambush predator, and *Spartaeus* is a web-builder, but both *Phaeacius* and *Spartaeus* sometimes stalk moths similarly to *C. gibbosus*. A slow approach, followed by an attack by lunging from close range, is a practicable predatory tactic against moths sitting quietly on tree trunks, but appears comparatively ineffective against the faster moving insects on which salticids are more often portrayed as preying.

Coccalus gibbosus, for a salticid, has another unusual way of catching prey: it goes into alien webs to catch spiders and insects. In this, it resembles some other spartaeines—*Brettius*, *Cyrra*, *Gelotia*, and *Portia* (Jackson & Hallas 1986a, b; Jackson 1990a, d) which also invade alien webs. All of the web-invading spartaeines studied, including *C. gibbosus*, have the property of not adhering to either cribellate or cribellate glue in sticky webs. There is, however, an important difference between *C. gibbosus* and the other web-invading spartaeines: all except *C. gibbosus* are aggressive mimics that make specialised vibratory signals to trick the owner of the alien web. Although there are some non-spartaeine salticids that sometimes catch spiders and insects by leaping into or walking across alien webs (Jackson 1986), no non-spartaeine salticids are known to make vibratory aggressive mimicry signals in alien webs and none are known to be able to touch without adhering to sticky webs.

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- in the following order: species, family (plus order for insects), collection site, description, types of tests. (CS: spins cribellate sticky web. CU: non-salticid cursorial spider. ES: ecribellate sticky web. F: *C. gibbosus* put into cage with spider or insect, or spider or insect put in cage with *C. gibbosus*; cage free of nests and webs. I: Insect; all others, spiders. NE: eggs in vacant nest of cursorial spider. NO: nest occupied by cursorial spider, but no eggs present. NS: non-sticky web. SS: social species; builds communal web. TS: typical cursorial salticid. WB: web-building spider. WE: eggs in vacant web. WO: web occupied by host spider. WI: insect in vacant web of *Stegodyphus sarasinorum*. WV: vacant web with no eggs.
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- Araneus pustulosus* Araneidae. New Zealand. WB, ES, WO, WV.
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APPENDIX

Spiders and insects used as potential prey or as sources of eggs, webs and nests in tests with *Cocalus gibbosus*—listed alphabetically by species. Information will be given

Ambush predatory behaviour of *Phaeacius malayensis* and *Phaeacius* sp. indet., spartaeine jumping spiders (Araneae: Salticidae) from tropical Asia

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Abstract How jumping spiders from the spartaeine genus *Phaeacius* catch prey and use silk is considered. Behavioural data are provided for the first time for *Phaeacius malayensis* from Singapore and new behavioural data are given for *Phaeacius* sp. indet. from Sri Lanka. Both species are ambush predators and particularly proficient at catching moths and salticids. The behaviour of *Phaeacius* is compared to that of other studied spartaeines and the results of this study are discussed in relation to salticid evolution.

Keywords spiders; Salticidae; Spartaeinae; *Phaeacius*; predation; behaviour

INTRODUCTION

Salticids are one of the major animal groups in which acute vision has evolved, but the evolutionary origins of these spiders and their unique eyes remain poorly understood. Comparative studies of spartaeine salticids have been pivotal in recent discussions of salticid evolution. These salticids are morphologically unusual and, with respect to some characters, primitive (Wanless 1984). Recent ultrastructural studies are of particular interest, showing that many spartaeines have somewhat

poorly organised principal retinæ (Blest 1983, 1984, 1985, 1988; Blest & Sigmund 1984; Blest & Carter 1987, 1988; Blest et al. in press). In others (e.g., *Portia*), retinæ are orderly and sustain fine visual acuities. Spartaeines are also unusual behaviourally (Jackson & Hallas 1986a, b; Jackson & Pollard 1990; Jackson 1990 a, b, c). All species studied use silk in unusual ways. Typical salticids build cocoon-like silk nests, but spartaeines are known to build only large prey-catching webs, or silk platforms that appear like rudimentary webs.

Spartaeine predatory behaviour is atypical for salticids. All spartaeines studied rely primarily on lunging, instead of leaping, to attack prey. *Brettus*, *Cocalus*, *Cyrrha*, *Gelotia*, and *Portia* are specialised web-invaders that prey on other spiders and do not adhere to sticky webs. Each of these species, except for *Cocalus*, makes specialised aggressive mimicry signals.

Phaeacius is a genus of Asian spartaeines (Wanless 1981) and behavioural details are available for only one species, *Phaeacius* sp. indet. from Sri Lanka (Jackson & Hallas 1986b). This spider was shown to be a specialised ambush predator that sits on tree trunks and waits for its prey to come to it instead of adopting the typical salticid strategy of actively stalking then leaping on active insects. This paper is an extension of the earlier study. The behaviour of *Phaeacius malayensis* from Singapore is studied for the first time, and additional information is provided on the predatory behaviour of *Phaeacius* sp. indet. In particular, these two species are shown to be especially efficient predators of other salticids and moths.

MATERIALS AND METHODS

Observations were laboratory based, in conjunction with a few field observations. The laboratory culture used in this study consisted of 6 *Phaeacius malayensis* and 26 *Phaeacius* sp. indet. *P. malayensis* was collected in the Royal Botanic Gardens in Singapore and *Phaeacius* sp. indet. was collected from

Peradeniya in Sri Lanka. All specimens were either adults or large juveniles one or two moults from maturity.

Standard maintenance and testing procedures, terminology, and conventions for describing behaviours were followed (see Jackson & Hallas 1986a). The earlier study on *Phaeacius* sp. indet. was repeated on *P. malayensis*. This included each of the tests using each of the insects and spiders used in the earlier study (see Table 1 in Jackson & Hallas 1986b), except that *Stegodyphus sarasinorum* was used instead of *S. mimosarum*, *Zosis genicularis* was used instead of *Philoponella variabilis*, and there were no tests using *Tegenaria domestica* and *Trite planiceps*. Because the two species were found to be very similar in behaviour, the term "*Phaeacius*" will be used whenever it is not essential to distinguish between the species.

Having observed *Phaeacius* feeding especially often on other species of jumping spiders and on moths in nature, laboratory tests were carried out to compare how efficiently *Phaeacius* caught these and other types of prey. The spiders and insects (Appendix 1) used were never more than about half the size of the *Phaeacius*. Only adults of the insects were used, but the spiders were both juveniles and adults.

Before each test, the *Phaeacius* was in an individual glass tank, resting on a vertical bark-covered log ("matching background") or a smooth vertical wooden board ("non-matching background") inside the tank (see Jackson & Hallas 1986b). The logs and boards were c. 100 mm in diameter. Because testing procedure was similar to "Type A" tests in an earlier study of *Portia* (Jackson & Hallas 1986a), only essential details about methodology are given here.

All tests were paired, each *Phaeacius* being presented with one type of prey one day and another type the next day, in random order. Each test began when prey was put in the cage shortly after lights came on in the laboratory (0800 h). The *Phaeacius* was watched continuously until it caught a prey or until 4 h had elapsed. If *Phaeacius* had not caught a prey after 4 h the test ended and all prey were removed from the cage.

When testing *Portia* only a single prey item was used during each test. This was impracticable when testing *Phaeacius*, because this ambush predator in its large cage rarely caught a lone prey item in a 4 h test. The test procedure was modified for *Phaeacius*. Although only one species of prey was presented to *Phaeacius* in a given test (except for moths: see

below), the number of individuals of the prey species was made sufficient to assure that some came close to the *Phaeacius* during the test period: 5–10 jumping spiders per test; 15–30 hunting spiders per test; 5–10 flies per test. Two species of moths were available (Appendix 1). Whenever testing with moths, both species were put in the cage: 10–15 of each species per test.

Only one prey-capture was allowed in these tests. Once *Phaeacius* began feeding, or after 4 h elapsed if *Phaeacius* failed to catch a prey, all remaining prey were removed from the cage.

Because each individual *Phaeacius* was always tested with two types of prey, but in random order, data were compared using McNemar tests for significance of changes. No individual *Phaeacius* was used more than once for tests with any pair of prey species (except for moth vs fly), but each individual was tested with a range of pairs of prey species. Each individual was used in two moth vs fly test pairs, 1–2 weeks apart. Data for *P. malayensis* and *Phaeacius* sp. indet. were pooled because the test results gave no suggestion of differences between these species.

OBSERVATIONS

Moulting and ovipositing

Phaeacius spun a small (about twice the body length of the spider in diameter), flimsy, horizontal, or vertical silk sheet when it moulted and oviposited. These "nests" were not built at any other times. Eggsacs were placed against the substrate under the nest. Only one *P. malayensis* and three *Phaeacius* sp. indet. oviposited in the laboratory, and no egg-sacs were seen in nature. Each was under a vertically-oriented nest, but the female each time ate the eggs and destroyed the egg-sac soon after it was made. These four egg-sacs appeared similar to egg-sacs that have been described for other spartaneines, although they were not examined carefully.

Exoskeletons were found about equally often under vertically and horizontally oriented nests. One *P. malayensis* and two *Phaeacius* sp. indet. were seen in the process of moulting. Each had a horizontal nest suspended only 1–4 mm below the top surface of the cage. The spider hung upside down from the platform while moulting (i.e., the silk sheet was between the spider and the cage). After moulting, the exoskeleton hung down by draglines from the nest, while the spider stood on the substrate between the silk and the cage.

Morphology, posture, and eucrypsis

Like most spartaeines, but in contrast to most other alticids, *Phaeacius* has functional postero-medial eyes. *Phaeacius* is more dorso-ventrally flattened than most spartaeines, which appears to be related to this spider's habit of resting on tree trunks. *Phaeacius* adopted a special posture, the "flattened posture", when at rest. On a vertical surface, facing downward, the body, legs, and palps were pressed against the substrate, with legs I–III angled forward and legs IV angled rearward. The spider's palps angled forward and converged so that the tips of their tarsi were only 1–2 mm apart; the palps of males also angled forward, but diverged outward at an angle of 10–20°. *P. malayensis* and *Phaeacius* sp. undet. were similar looking. Both had moderately long, robust, and spiny legs and a hirsute body with dull grey and brown markings that resembled the surface of tree trunks in the Asian rainforest. Sexual dimorphism was not pronounced in *Phaeacius*, the two sexes being similar in general appearance and size. Males were not used in tests of predatory behaviour because they sometimes appeared to be less responsive than females and large juveniles to prey, but the predatory behaviour used by males was the same as that of females and juveniles.

Locomotion

Unlike most salticids, *Phaeacius* did not often walk about spontaneously. When it did occasionally move spontaneously, *Phaeacius* usually stepped slowly and steadily in a more or less straight forward direction and continued to advance for many seconds at a time, in doing so covering 300 mm or more. The spider's body was raised somewhat off the substrate while walking, and legs I were not extended as far forward as when in the flattened posture. Otherwise, the walking posture was not greatly different from the flattened posture.

Phaeacius occasionally waved its palps up and down in matching phase when standing between bouts of stepping, but it did not perform distinct leg and palp waving as it walked. *Phaeacius* did, however, flick legs I and II while walking. "Flicks" were rapid, low amplitude up-and-down movements, the leg leaving the substrate at the start and returning at the end of the flick.

When stimulated (e.g., touched with a brush), *Phaeacius* generally just remained stationary in the flattened posture, although it sometimes twitched the leg that was touched or pulled its palps back closer to the chelicerae. Considerable harassment

was needed to provoke *Phaeacius* into decamping, but once provoked it ran away in a strikingly unusual fashion for a salticid. After pulling its legs in closer to the body, it usually ran rapidly 100–300 mm in a straight line. At the end of the run, it stopped suddenly and adopted the flattened posture, although the palps usually remained close to the chelicerae for several minutes before being slowly extended. Then, about 10 min later, *Phaeacius* walked away.

Tests with webs, eggs, and nests of other spiders

Phaeacius never entered webs voluntarily. If it contacted the edge of a web accidentally, *Phaeacius* moved away immediately. If dropped on a non-sticky web, it dropped out of the web immediately, without fastening a dragline, or walked with evident difficulty (tripping on lines or slipping off lines) to the edge. *Phaeacius* stuck to cribellate and ecribellate sticky webs on which it was dropped. It was able to free itself by biting at threads and pulling forcefully with its legs and then dropping out of the web or laboriously walking to the edge of the web. However, *Phaeacius* was unable to free itself from the exceedingly sticky web of *S. sarasinorum*. *Phaeacius* did not respond to the eggs or nests of other spiders.

Ambush predation

Phaeacius was unusually sedentary for a salticid and usually stood inactive in the flattened posture for many hours, if not days, at a time. *Phaeacius* often remained quiescent while insects or spiders moved about in the vicinity. When an insect or spider walked over *Phaeacius'* legs or body, there was usually either no overt response or merely a brief twitching of the contacted legs.

Generally, prey was not attacked until it walked between tarsi of *Phaeacius'* legs I. *Phaeacius* attacked by making a sudden, extremely rapid lunge forward to grasp the prey. During the lunge, the spider's body was propelled upward 2–3 mm and forward about half a body length. *Phaeacius* sometimes slowly shifted legs I–III more forward and inward before the lunge, but often there were no obvious preliminaries. The lunge finished with *Phaeacius* standing over the prey with fangs inserted and often legs I and II forming a "basket" around the prey (the ventral surfaces of the tarsi and, sometimes, metatarsi being in contact with the prey). Legs were usually moved away from the prey after

Table 1 Results from testing *Phaeacius* on alternate days with different types of prey. Matching background.

Test pair	Caught no. 1 only	Caught no. 2 only	Caught both	Caught neither
<i>Bavia sexpunctata</i> Moth	3	1	2	23
<i>Bavia sexpunctata</i> Fly	2	0	4	20
<i>Colopsus cancellatus</i> Moth	3	2	3	22
<i>Colopsus cancellatus</i> Fly	10	0	2	19
<i>Plexippus culicivorus</i> Moth	5	2	2	22
<i>Plexippus culicivorus</i> Fly	3	0	1	28
<i>Plexippus culicivorus</i> <i>Clubiona cambridgei</i>	8	0	2	22
<i>Sandalodes remicupreus</i> Moth	5	2	1	20
<i>Sandalodes remicupreus</i> Fly	2	0	1	22
<i>Thorellia ensifera</i> Moth	4	1	4	23
<i>Thorellia ensifera</i> Fly	12	0	1	19
<i>Thorellia ensifera</i> <i>Anzacia gemmea</i>	5	1	1	22
Moth <i>Anzacia gemmea</i>	3	0	4	20
Moth <i>Clubiona cambridgei</i>	5	1	0	24
Fly <i>Anzacia gemmea</i>	0	3	3	24
Fly <i>Clubiona cambridgei</i>	1	1	3	25
Moth Fly	9	1	2	58

Table 2 Summary data from testing *Phaeacius* on alternate days with different types of prey. Matching background.

Test pair	Caught no. 1 only	Caught no. 2 only	Caught both	Caught neither	McNemar tests*
Jumping spider Moth	20	8	12	110	$P < 0.05$
Jumping spider Fly	29	0	9	108	$P < 0.001$
Jumping spider Hunting spider	13	1	3	44	$P < 0.001$
Moth Fly	9	1	2	58	$P < 0.05$
Moth Hunting spider	8	1	4	44	$P < 0.05$
Fly Hunting spider	1	4	6	49	NS

*Compares numbers in first two columns only (see Sokal & Rohlf 1981).

no more than a few seconds. At the end of the lunge, legs III were out about perpendicular to the sagittal plane of the body, legs IV were extended more or less straight back, and the palps were pulled back to beside the chelicerae. *Phaeacius* resumed the flattened posture at about the time when the prey ceased to struggle vigorously, except that its palps remained pulled back beside the chelicerae as it fed.

Active pursuit of insects by *Phaeacius*

If an insect became more or less stationary a few centimetres away from a facing, flattened *Phaeacius*, the spider sometimes approached in a characteristic manner, stepping slowly, rocking, and preserving its flattened posture. To rock, the spider's body moved about half a body length forward then, without pausing, moved smoothly back, but not quite all the way to the original position. Legs were pulled in somewhat closer to the body during rocking, and they made almost imperceptibly short steps that advanced the spider toward the insect. If the prey remained stationary, *Phaeacius* got to within about half a body length and lunged, or it became quiescent and later lunged when the insect moved past.

Predation on salticids by insinuation

Sometimes a *Phaeacius* appeared to take a particular interest in salticids walking about in its vicinity. *Phaeacius*' behaviour (referred to as "insinuation") in these instances was distinctive and has not been described previously.

Beforehand, *Phaeacius* remained quiescent in the flattened posture for a long period, sometimes for over an hour, while a salticid walked about in its vicinity. Then, suddenly, *Phaeacius* turned as much as 180° and faced the active salticid. Immediately *Phaeacius* completed the turn, the flattened posture was resumed. After several minutes, *Phaeacius* might turn toward the salticid again or it might walk a few millimetres slowly toward the salticid.

By repeatedly stepping a few millimetres at a time toward the salticid, interspersed with long pauses in the flattened posture and occasional sudden turns, *Phaeacius* moved into the area in which the salticid was active.

Once close to the salticid, *Phaeacius* tended to stay in the rest posture facing the salticid. Additional sudden flattened might be made to keep facing a salticid that moved about. If the salticid moved farther away, *Phaeacius* might intermittently walk

again to stay close. If the salticid walked directly in front of *Phaeacius*, *Phaeacius* lunged and caught it.

Insinuation was seen only when the salticid was active in a localised area. Instances in which the salticid was grooming a lot were especially likely to elicit insinuation from *Phaeacius*.

Test results

On matching background, *Phaeacius* caught salticids more often than it caught moths, flies, or hunting spiders and it caught moths more often than it caught flies or hunting spiders (Tables 1, 2). There was no evident difference, however, in how often it caught flies and hunting spiders.

On non-matching background, *Phaeacius* caught moths more often than it caught jumping spiders, hunting spiders, or flies. There were no evident differences in frequencies of catching jumping spiders v. flies, jumping spiders v. hunting spiders, or flies v. hunting spiders (Tables 3, 4).

Phaeacius caught jumping spiders more often on matching than on non-matching background (Table 5). There was no evidence that background affected how often *Phaeacius* caught any other type of prey.

DISCUSSION

Spinning behaviour, moulting, and oviposition

Typically, salticids build cocoon-like nests in which they rest, moult, and oviposit; *Phaeacius* did not. *Portia* and *Spartaeus* are web-building spartaeines. *Phaeacius* resembles the other known spartaeines by being, in some respects, intermediate between the web-builders and the nest-builders. These "intermediates" spin small, web-like resting structures and oviposit under, or hanging from, these.

Locomotion and crypsis

Salticids typically have a rapid stop-and-go gait, change directions frequently while they walk, pivot about between stepping bouts, jump across obstacles, and wave their legs and palps a lot. All spartaeines, however, have atypical styles of locomotion, *Phaeacius* being one of the most unusual.

Markings and flattened shape made *Phaeacius* difficult to distinguish from its background ("eucrypsis", Robinson 1969) when it rested on a tree trunk. Generally, *Phaeacius*' style of

locomotion helped maintain eucrypsis. Presumably, eucrypsis is significant in protecting *Phaeacius* from visually hunting predators.

Predatory behaviour

Forster (1977) analysed in detail the typical predatory sequences of active visually hunting salticids. The first phase of predation, "orientation", consists of three distinct stages: "alert", "swivel" (cephalothorax pivoted so that the principal eyes face the prey), and "align" (abdomen moved into alignment with the cephalothorax). For the next

phase, "pursuit", there are three alternatives: "walk", "run" (prey rapidly chased), and "stalk" (salticid slowly advances toward the prey). There are three stages in the final phase, "attack-capture": "precrouch" (a pause), "crouch" (body pressed close to the substratum), and "jump" (by extending legs III and IV, the spider is propelled onto the prey). No spartacines are known to have predatory behaviour that resembles closely that of typical salticids. All attack prey primarily by lunging instead of leaping and the sequences preceding attack never fully correspond to Forster's description for typical salticids.

Table 3 Results from testing *Phaeacius* on alternate days with different types of prey. Non-matching backgrounds.

Test pair	Caught no. 1 only	Caught no. 2 only	Caught both	Caught neither
<i>Bavia sexpunctata</i> Moth	1	4	0	24
<i>Bavia sexpunctata</i> Fly	0	0	2	26
<i>Colopsus cancellatus</i> Moth	0	2	2	23
<i>Colopsus cancellatus</i> Fly	2	0	1	25
<i>Plexippus culicivorus</i> Moth	1	2	0	27
<i>Plexippus culicivorus</i> Fly	1	0	3	26
<i>Plexippus culicivorus</i> <i>Clubiona cambridgei</i>	1	0	0	27
<i>Sanalodes remicupreus</i> Moth	1	5	0	21
<i>Sanalodes remicupreus</i> Fly	1	0	1	27
<i>Thorellia ensifera</i> Moth	1	6	1	21
<i>Thorellia ensifera</i> Fly	2	1	0	26
<i>Thorellia ensifera</i> <i>Anzacica gemmea</i>	1	0	2	27
Moth <i>Anzacica gemmea</i>	10	0	3	18
Moth <i>Clubiona cambridgei</i>	3	0	3	25
Fly <i>Anzacica gemmea</i>	1	0	3	28
Fly <i>Clubiona cambridgei</i>	2	0	2	26
Moth Fly	15	2	1	46

Phaeacius is especially atypical. This spider is highly specialised ambush predator which is specially proficient at catching moths and salticids. Even it remains absolutely quiescent until the moment of attack. When it does approach the prey, it does so slowly and in a way that maintains crypsis. Being extremely eucryptic and being specialised as an ambush predator, the question arises of whether eucrypsis is a specialisation related to concealment from prey instead of, or (more probably) in addition to, concealment from predators.

The experiments comparing prey capture rates on matching v. non-matching background appear to indicate that visual concealment is important in respect to some, but not all, prey: salticids were caught more often when background was matching than non-matching, but background had no effect in tests with other types of prey. Salticids, having well-developed acute vision, tend to see the

Phaeacius and recognise it as a potential predator when background is non-matching but not when it is matching.

Phaeacius sometimes simply waited until salticids came close then ambushed them. However, *Phaeacius* also had a special behaviour, insinuation, by which it put itself in a place from which it was more likely to be able to ambush a salticid.

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Table 4 Summary data from testing *Phaeacius* on alternate days with different types of prey. Non-matching background.

Test pair	Caught no. 1 only	Caught no. 2 only	Caught both	Caught neither	McNemar test*
Jumping spider Moth	4	19	3	116	$P < 0.001$
Jumping spider Fly	6	1	7	130	NS
Jumping spider Hunting spider	2	0	2	54	NS
Moth Fly	15	2	1	46	$P < 0.001$
Moth Hunting spider	13	0	6	43	$P < 0.001$
Fly Hunting spider	3	0	5	54	NS

*Compares numbers in first two columns only (see Sokal & Rohlf 1981).

Table 5 Comparison of rate at which *Phaeacius* caught different types of prey on matching or non-matching backgrounds. Data from Tables 2 and 4.

Prey type	Background	No. of tests	No. caught	Test of independence
Jumping spider	matching	262	86	$P < 0.001$
	non-matching	300	24	
Moth	matching	212	43	NS
	non-matching	205	57	
Hunting spider	matching	137	19	NS
	non-matching	154	13	
Fly	matching	215	19	NS
	non-matching	230	16	

were provided by the New Zealand Ministry of Agriculture and specimens have been deposited at the British Museum (Natural History).

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APPENDIX I

Spiders and insects used as potential prey in tests using *Phaeacius malayensis* and *Phaeacius* sp. indet. listed alphabetically by species. Information will be given in the following order: species, family (plus order for insects), collection site, description. Hunting spider: not a salticid. Jumping spider: typical cursorial salticid, sympatric with *Phaeacius* and known to go on to tree trunks in nature.

Anzacica gemnea. Gnaphosidae. New Zealand. Hunting spider. *Bavia sexpunctata*. Salticidae. Sri Lanka. Jumping spider. *Clubiona cambridgei* (L. Koch). Clubionidae. New Zealand. Hunting spider. *Colopsus cancellatus*. Salticidae. Sri Lanka. Jumping spider. *Ctenopseustis* sp. Lepidoptera, Tortricidae. New Zealand. Moth. *Melanchna* sp. 1. Lepidoptera, Noctuidae. New Zealand. Moth. *Musca domestica* (L.). Diptera, Muscidae. Culture. Fly. *Plexippus culicivorus*. Salticidae. Sri Lanka. Jumping spider. *Sandalodes remicupreus*. Salticidae. Sri Lanka. Jumping spider. *Thorellia ensifera*. Salticidae. Singapore. Jumping spider.

Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrhothele antipodiana* (Araneae: Hexathelidae) and a literature review

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Abstract This is the first comprehensive behavioural study of intraspecific interactions of *Porrhothele antipodiana*, a large web-building mygalomorph spider which is endemic to New Zealand. A special posture in which the spider raises its body and extends its fangs ("gaping display") appears to be primarily an antipredator defence and is only infrequently adopted by *P. antipodiana* in intraspecific interactions. *P. antipodiana* uses eight major displays (chewing, grappling, clasping, nipping, palpating, probing, tabbing, and tugging) during intraspecific interactions, palpating being predominant. Males use claspers on legs I to hold onto females during copulation. Females become passive when clasped. Cannibalism is rare; when it does occur, males kill females about as often as females kill males. From comparison of results from a variety of testing procedures, there is no evidence that studying interactions of *P. antipodiana* in the laboratory seriously distorts this species' behaviour. The literature on intraspecific interactions, especially courtship, of other mygalomorphs is reviewed. The function of mygalomorph courtship is discussed, special attention being given to the significance of cannibalism and the role of the male's behaviour of clasping females.

Keywords spiders; *Porrhothele antipodiana*; displays; courtship; mating behaviour; cannibalism

INTRODUCTION

Most spiders belong to either the "primitive", and usually large, Mygalomorphae or the "modern", usually small, Araneomorphae. Intraspecific interactions of araneomorph spiders have received considerable attention, but there have been few detailed studies of how mygalomorphs interact. A common impression seems to be that the mygalomorphs, being primitive, have simple repertoires of behaviour (Gerhardt 1929; Platnick 1971; Main 1976; Foelix 1982).

Raven (1980) pointed out that because mygalomorphs have plesiomorphic features, studies of these spiders can provide important perspective to evolutionary hypotheses. Raven (1984) has been instrumental in generating interest in mygalomorph systematics and biogeography, but research on mygalomorph behaviour has lagged behind.

New Zealand has an abundant mygalomorph fauna with over 100 species in 3 families and 5 genera (Forster & Wilton 1968). *Porrhothele antipodiana* is, by weight, New Zealand's largest spider and is probably New Zealand's most widely distributed mygalomorph, being found from subalpine to coastal regions throughout the North and South Island. *P. antipodiana* is most commonly found on the ground surface beneath loosely fitting stones and rotting logs, where it builds a web consisting of a narrow silk tube opening onto a large sheet web (Todd 1945).

Forster & Forster (1973) provided a general account of *P. antipodiana*'s natural history, and Butt & Taylor (1985) investigated this species' salt and fluid balance physiology. The most extensive studies, however, have been carried out by Laing (1973, 1975, 1978, 1979, 1982) on a North Island population in the vicinity of Wellington. Laing investigated population dynamics, predators and prey, predatory behaviour, and antipredator behaviour, but there have been no detailed studies of this species' intraspecific interactions and display behaviour.

P. antipodiana was in the Dipluridae (Forster & Wilton 1968; Raven 1978) until Raven (1980) put it in a newly erected family, Hexathelidae (Table

1). *Porrhothele*, a genus endemic to New Zealand, is closely related to *Atrax*, the infamous (sometimes deadly) "funnel web spiders" (Underhill 1988). Recently, using morphological and electrophoretic data, Gray (1988) put some of the species that were formerly in *Atrax* in a new genus, *Hadronychne*, and erected a new hexathelid subfamily, Atracinae, for these two genera.

MATERIALS AND METHODS

Study site and population census

Our field site was on the Kaikoura Peninsula (190 km north of Christchurch), 10–15 m from the shoreline. The spiders were in webs beneath loosely fitting stones. We estimated the density of *P. antipodiana* in this population by carrying out a

census in a 5 × 5 m area in a part of the habitat in which we had not previously collected. We turned over all the stones in this area and recorded the sex and body length of each spider found.

General methodology

Standard maintenance, analysis, terminology, and testing procedures were used (see Jackson & Hallas 1986). This included the convention that expressions such as "usually" or "generally", "sometimes" or "occasionally", and "infrequently" or "rarely" are used to indicate frequencies of occurrence of about 80% or more, 20–80%, and 20% or less, respectively. "Male" and "female" refer to adult animals only, all others being "juveniles" with no reference to sex, the sex of juveniles being difficult if not impossible to ascertain.

Table 1 Taxonomy and distribution of the mygalomorph family Hexathelidae (from Raven 1980).

Subfamily	Genus	Distribution
Macrothelinae	<i>Porrhothele</i> <i>Atrax</i>	New Zealand Eastern Australia including Tasmania
Hexathelinae	<i>Macrothele</i> <i>Bymaaniella</i> <i>Hexathele</i> <i>Paraembolides</i> <i>Scotinoecus</i>	Eurasia and Africa South central coastal Australia New Zealand New South Wales and southern Queensland South America
Plesiothelinae	<i>Terania</i> <i>Plesiothele</i>	Southern Australia including Tasmania Tasmania

Table 2 Total number of tests of each type (see text) for each pairing of male (M), female (F), and juvenile (J) *Porrhothele antipodiana*. Forced encounters: tests with escape ramps in parentheses. Spontaneous encounters: Successful tests in parentheses. I: intruder. R: resident. See text for details.

			M(I)-F(R)	M(R)-F(I)	M-M	M(I)-J(R)	M(R)-J(I)	F-F	F(I)-J(R)	F(R)-J(I)	J-J
Forced encounters	Normal photoperiod	Plastic boxes	52 (10)	12 (5)	45 (6)	24 (5)	7 (4)	20 (5)	15 (4)	12 (5)	22 (8)
		Glass tanks	18	0	14	9	0	12	10	12	12
	Reversed photoperiod	Plastic boxes	17 (10)	9 (0)	20 (10)	15 (10)	5 (0)	20 (10)	12 (0)	10 (0)	16 (10)
		Glass tanks	10	0	0	0	0	10	8	10	0
Spontaneous encounters	Normal photoperiod	Modular cages	35 (32)	2 (2)	17 (16)	10 (10)	0	13 (7)	20 (4)	6 (6)	35 (13)
		Glass tanks	13 (11)	0	0	0	0	19 (8)	0	0	25 (7)
	Reversed photoperiod	Modular cages	28 (28)	2 (2)	26 (26)	23 (22)	3 (3)	28 (11)	15 (3)	6 (6)	24 (9)
		Glass tanks	18 (18)	0	0	0	0	26 (6)	0	0	21 (5)
Total no. of tests			191	25	122	81	15	148	80	56	155
Total no. of successful tests			186	25	121	80	15	94	52	56	84

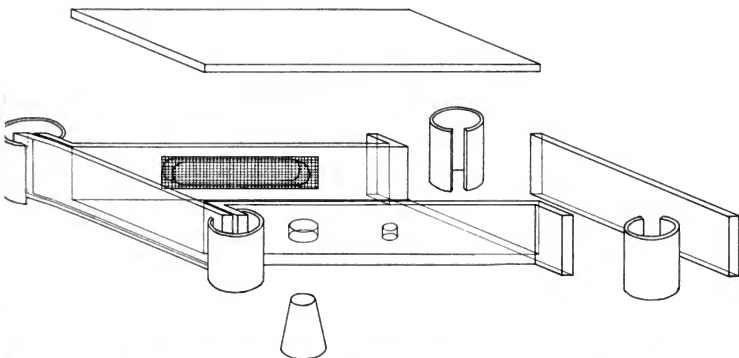


Fig. 1 "Exploded" drawing of transparent perspex "modular cage". Removable glass top. Removable perspex end pieces held in place by plastic clamps. Wire mesh screening on two sides (only one shown). One large and two small (only one on right shown) holes plugged by corks (only large cork shown) on bottom of cage.

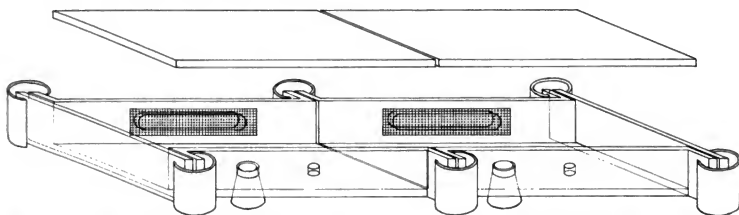


Fig. 2 Drawing of two joined modular cages. Tops removed in drawing. Wire mesh shown on only one side. Only one (on right) of the two small cork holes shown on each cage.

Males and females are c. 15 mm and 20 mm in body length, respectively. Juveniles used in this study were 10–15 mm in body length. Juveniles used in juvenile-juvenile interactions were about equal to each other in size.

All interactions were staged on webs built in plastic cages or glass tanks. A resident spider was allowed at least 10 days to build a web. Females and juveniles spun dense sheets and tunnels during this period, but males were less likely to spin, usually making only a sparse sheet with no tunnel. We were able to test males in their own webs,

however, by putting them into cages as juveniles. We then tested the males after they matured in the dense webs they built as juveniles in these cages.

The individuals in a pair were never tested together more than once, although a given individual might be tested several times with different individuals. No individual was used in more than one test on a given day or more than once in a test of any given type.

Some tests were carried out in a room with a reversed photoperiod (12L:12D; lights off: 0800 h). "Night-time" in this room was kept under dim

illumination rather than total darkness. The spiders were left in this room for 10–14 days before testing, allowing them to adjust to the reversed photoperiod. All other tests were carried out in a room with “normal” non-reversed 12L:12D photoperiod (lights on: 0800 h).

Tests of intraspecific interactions

Laboratory tests began when one spider (the “test-spider”) contacted the web of the other spider (the “resident-spider”). The test-spider, after being prodded with a brush out of its own web, was dropped onto the resident’s web (“forced encounters”) or allowed to enter the resident’s web spontaneously (“spontaneous encounters”). For most tests with forced encounters, the resident was in a web in a plastic box (approximate size: 140 cm² bottom surface area and 7 cm deep). A smaller number of forced encounter tests were with the resident in a web in a glass tank (bottom surface area 1250 cm² and 25 cm deep).

Two methods were used for staging spontaneous encounters (Table 2).

- 1 Each spider was allowed to build its web in a “modular cage” (Fig. 1, 2). The spiders were watched after joining two modular cages end to end, a test beginning when one spider entered the web of the other. Modular cages were kept closed, but a spider could readily leave a web by walking into the attached cage.
- 2 Two ordinary cages, each containing a spider in its web, were placed c. 10 cm apart near the centre of the bottom of a glass tank. The bottom of the tank was covered by sand and the cages were buried so that their tops were level with the sand. Immediately the cages were buried, their lids were removed. A 20 cm wide (50 cm long) stiff sheet of perspex was placed in each cage to make a ramp from the web to the sand on the side closest to the other cage. Spiders readily walked in and out of webs using these ramps.

Observations were terminated after 6 h if neither spider entered the web of the other. Observation was terminated earlier if both spiders left their webs. Instances in which observations were terminated before one spider entered the occupied web of another were referred to as “unsuccessful tests”. (By definition, all forced encounters tests were “successful”.)

In all tests, spiders could leave the resident’s web. During testing, tanks and plastic boxes were left open (tops removed). Spiders could not escape from the tanks, however, because they could not

climb the glass sides but, because the tanks were bigger than the webs, the spiders could leave the web without having to leave the tank. Spiders sometimes had difficulty climbing out of the plastic boxes but an “escape ramp” was in place to help them. Just before the test began a stiff sheet of perspex (c. 20 mm wide and c. 50 mm long) was positioned with one end on the web and the other leaning against the side of the open cage. Spiders readily climbed up these ramps to leave cages.

Spiders were watched until one spider left the cage, one spider killed the other, a male-female pair mated, or 2 h elapsed. If the spiders were mating or otherwise “actively interacting” after 2 h, observation continued until mating ended or the spiders became quiescent. Spiders were said to “actively interact” (Table 3) if, during the test, there was physical contact, chasing, grappling, injury, cannibalism, mating, or palpating.

RESULTS

Population census

We found 65 spiders in the census area, males, females, and juveniles comprising 9%, 11%, and 80%, respectively, of the sample. This was a dense population (2.6 spiders per m²), comparable to the North Island populations studied by Laing (1978).

Elements of behaviour

Each element of behaviour will be described below, and the contexts in which displays occurred will be indicated in Tables 4–7.

Normal palp posture. Palps were held anterior and slightly lateral to the chelicerae, with femora angled sharply up and the rest of the palp sharply down (Fig. 3). Palps were sometimes angled laterally c. 15° from the femur-patella to the tarsus.

Retracted palp posture. Palps were held to the sides of the chelicerae, femur angling up and the rest of the palp angling down.

Raised palp posture. Palps were elevated above the chelicerae as a result of movement of the femur. Femur-patella and tibia-metatarsus joints were held about the same as in the normal posture.

Palpate. Palpating, the most common and distinctive behaviour (Table 7) during intraspecific interactions, made the silk move conspicuously within a radius of c. 40 mm of the spider. Usually, the two palps moved up and down in more or less alternating phase (Fig. 4, 5), appearing to step in place, although

Table 3 Tests in which spiders did not actively interact. Comparison of different testing procedures.

			Male- Female	Male- Male	Male- Juvenile	Female- Female	Female- Juvenile	Juvenile- Juvenile
Forced encounters Both photoperiods	Plastic boxes, Escape ramp	No. of tests	25	16	19	15	9	18
		Did not actively interact	12%	6%	16%	13%	22%	17%
	Plastic boxes, no escape ramp	No. of tests	65	49	32	25	40	20
		Did not actively interact	6%	8%	6%	4%	13%	5%
	Glass tanks	No. of tests	28	14	9	22	40	12
		Did not actively interact	4%	21%	56%	9%	15%	33%
	Normal photoperiod	No. of tests	67	53	31	27	40	26
		Did not actively interact	7%	13%	19%	11%	10%	19%
Both types of cages No escape ramp	Reversed photoperiod	No. of test	26	10	10	20	40	6
		Did not actively interact	0	0	10%	0	17%	0
Spontaneous encounters Both types of cages	Normal photoperiod	No. of successful tests	45	16	10	15	10	20
		Did not actively interact	2%	0	20%	13%	0	15%
	Reversed photoperiod	No. of successful tests	48	26	25	17	9	14
		Did not actively interact	6%	8%	4%	0	11%	0
Total no. of successful tests			211	121	95	94	108	84
Did not actively interact			8%	14%	21%	11%	23%	19%

Table 4 Performance of different behaviours by males in different kinds of interactions (See Table 2). Number: successful tests of each type. Percentage of each type of test in which each behaviour occurred is indicated.

	Male (I)-Female (R)	Male (R)-Female (I)	Male-Male	Male (I)-Juvenile (R)	Male (R)-Juvenile (I)
Number	186	25	121	80	15
Chase	5%	0	26%	54%	40%
Chew	41%	12%	10%	16%	0
Gaping display	1%	0	4%	0	0
Grapple	43%	16%	47%	27%	7%
Clasp	30%	8%	28%	15%	7%
Injure but not kill other spider	3%	4%	3%	1%	0
Kill other spider	4%	0	2%	11%	0
Lunge	26%	36%	15%	4%	0
Mate	26%	8%	0	0	0
Nip	26%	8%	0	0	0
Palpate	69%	44%	79%	44%	7%
Probe	22%	16%	18%	11%	0
Spin	47%	64%	41%	22%	13%
Stab	3%	0	3%	3%	0
Tear silk	29%	4%	5%	9%	0
Tug	18%	8%	16%	11%	0

the spider might palpate briefly with just one palp. Velocity and amplitude varied considerably (0.5–2/s; 5–20 mm), but there was a tendency for palpating to begin slowly and at low amplitude, then speed up and increase in amplitude. As a palp moved down, it usually contacted the silk, deflecting the web surface several millimetres. While a palp was moving up, silk usually adhered to tarsal setae and was pulled along for several millimetres, usually snapping loose before the palp reached its most dorsal position. Upward motion was sometimes slower than downward.

Usually, when the palp reached its most ventral position, there was a brief pause (c. 0.5 s) before

direction was reversed, but there were no pauses when changing direction at the most dorsal position. While one palp paused, the other palp continued moving and, because of this, phasing of the movements of the two palps was generally out of synchrony. Sometimes, when palpating at a rapid rate, there was no pausing at either the most dorsal or the most ventral position in the cycle and the movement of the two palps stayed synchronised. Because the down motion was faster than the up motion, palps appeared to pound down on the silk forcefully. This was especially true in male-male interactions.

While palpating, the spider usually held its palps 1–2 mm more to the side than usual (compare Fig.

Table 5 Performance of different behaviour by females in different kinds of interactions (See Table 2). Number: successful tests of each type. Percentage of each type of test in which each behaviour occurred is indicated.

	Female (R)- Male (I)	Female (I)- Male (R)	Female- Female	Female (I)- Juvenile (R)	Female (R)- Juvenile (I)
Number	186	25	94	52	56
Chase	34%	16%	47%	40%	52%
Chew	5%	8%	10%	2%	0
Gaping display	10%	0	2%	0	0
Grapple	43%	16%	31%	6%	9%
Injure but not kill other spider	4%	0	7%	0	2%
Kill other spider	3%	0	14%	4%	7%
Lunge	38%	20%	16%	2%	5%
Mate	26%	8%	0	0	0
Palpate	7%	0	10	2%	0
Passive state	26%	8%	0	0	0
Spin	30%	16%	61%	17%	20%
Stab	11%	0	5%	0	2%
Tear silk	6%	0	5%	2%	0
Tug	1%	0	0	0	0

Table 6 Performance of different behaviour by juveniles in different kinds of interactions (See Table 2). Number: successful tests of each type. Percentage of each type of test in which each behaviour occurred is indicated.

	Juvenile (R)- Male (I)	Juvenile (I)- Male (R)	Juvenile- Female	Juvenile (I)- Female (R)	Juvenile (R)- Juvenile (I)
Number	80	15	52	56	84
Chase	25%	20%	37%	18%	42%
Chew	1%	7%	0%	5%	8%
Grapple	27%	7%	6%	9%	37%
Injure but not kill other spider	1%	0	0	0	14%
Kill other spider	3%	0	0	0	8%
Lunge	13%	0	4%	0	14%
Palpate	4%	0	0	4%	27%
Spin	20%	13%	27%	34%	36%
Stab	4%	0	0	4%	2%
Tear silk	3%	0	0	2%	7%
Tug	0	7%	0	0	2%



Fig. 3 *P. antipodiana* female in normal rest and walking posture. Palps hang loosely in front of chelicerae.



Fig. 5 *P. antipodiana* male (top view) palpatory. Spider's left palp moving up; right palp moving down.

3, 5) but, otherwise, in about the normal posture. Sometimes, tarsi angled straight down, and palpatory was a simple dorso-ventral motion in which the palps remained perpendicular to the web. More often, palp tarsi moved in a rotary fashion and traced ellipses. This was brought about by a backward-and-forward motion superimposed on the up-and-down motion such that tarsi angled back as much as 45° while moving up and forward as much as 45° while moving down.

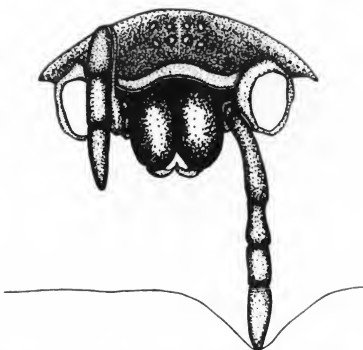


Fig. 4 Drawing of *P. antipodiana* palpatory. Head-on view. Legs absent from drawing for clarity. Palps "step in place". Spider's left palp pushing silk down.

While palpatory, the spider sometimes held its palps to the sides by as much as 45° . In this position, the palps moved up and down with or without the superimposed backward and forward rotary motion. As a palp moved up, its lateral deflection tended to decrease so that its motion became complex (i.e., both side-to-side and backward-and-forward motion might be superimposed simultaneously on the basic up-and-down motion). The forward-and-backward and lateral deflections of the two palps were usually comparable, but sometimes this was not true, making palp motion even more complex. Palpatory bouts were highly variable in duration, ranging from only a few seconds to several minutes. During pauses between bouts, palps usually returned to the normal posture.

Spiders were usually stationary when palpatory, although they sometimes slowly walked about while palpatory. A common pattern was for the spider to palpate briefly, then step forward a few millimetres as soon as it stopped palpatory, and so forth. *P. antipodiana* normally kept its body lowered and lying on the silk when stationary, but raised several millimetres when walking. Sometimes, when palpatory while walking, the palps failed to contact the silk. Also, spiders sometimes began to palpate just after separating after a grappling match (see below); in these instances, palps often did not contact the silk. When palps failed to contact the silk, there was no pause when the palps reversed direction at the lowest point in the cycle.



Fig. 6 *P. antipodiana* male (facing left) probes on silk over tunnel with legs I. Female in tunnel below male's legs I.



Fig. 7 Probing *P. antipodiana* male (facing left) moves to directly over female in tunnel (see Fig. 6).



Fig. 8 Pair of *P. antipodiana* males grapple. Spiders venter to venter, with bodies pushed up. Dorsal view of closer male. Fangs of other male partially extended and palps raised.

Stab. A spider stabbed by forcefully penetrating the web with extended fangs. It did this by suddenly flexing its legs to bring its body and extended fangs against the silk. Stabs were usually aimed at the other spider. When one spider was inside and the other was outside the tunnel, either spider might stab at the other. When spiders inside tunnels stabbed, their fangs were often seen coming through the silk to the outside. Despite the fierce appearance of this behaviour, no injuries were ever observed.

Chew. With its fangs penetrating the silk, a spider chewed by repeatedly opening and closing its chelicerae (1–2/s). A chewing spider usually had its legs highly flexed and its face pressed against the silk. Spiders often alternated between chewing for several seconds then moving their faces somewhat away from the silk and palpating for several seconds.

Tug. After penetrating the silk with its fangs, a spider tugged by repeatedly extending and flexing its legs, thereby elevating and lowering its body to pull the silk up and down (1/s, 1–5 mm). A spider might tug once at a time or in bouts of up to five at a time. Sometimes, the spider paused for several seconds in the most dorsal position of a tug before lowering the silk, occasionally chewing during the pause.

Tear silk. A spider on the outside of a tunnel containing another spider tore silk by slowly extending its fangs and flexing its legs to lower its body, then inserting and closing its fangs around the silk. Next, the spider extended its legs and stepped backwards, ripping the silk quickly and seemingly easily. Sometimes the spider entered the tunnel via the hole it made.



g. 9 Pair of *P. antipodiana* males grapple. Spiders enter to venter, with bodies pushed up. Viewed more or less side-on. Dorsal body of male on left in view. Note extended fang of other male and raised palps.

rope. Only males probed, and only when no more than 30 mm from another spider (of either sex). To probe, the male forcefully moved legs I forward and backward in alternating phase (1/s, 2–5 mm). One or both legs were usually in contact with the silk (Fig. 6), causing the web to move. Occasionally, the tip of neither leg I contacted the silk and the two legs simply moved in the air.

Often a probing spider walked slowly forward toward the other spider (Fig. 6, 7). When it got close, the probing spider's legs contacted the other spider. This was always followed by grappling.

Grappling. Grappling spiders stood face-to-face with legs I and II extended and moving about in a rapid and irregular fashion. Palps were either retracted or extended (Fig. 8, 9), and fangs were usually extended (Fig. 9). Grappling had the appearance of great violence, the spiders sometimes ending up gripping each other with their chelicerae.

Grappling bouts sometimes lasted 1–2 min, but ~30 s was more common. Grappling ended when one or both spiders decamped or one spider killed and ate the other. Even when both spiders survived, one or both often bled when grappling ended.

Lunge. A spider lunged by slowly raising its body and legs I (Fig. 10), then rapidly moving forward and down against the other spider. The upward motion appeared smooth and took c. 1 s, but the downward motion took only c. 0.1 s and was sudden

and snap-like. Spiders were often already in contact before they lunged; if not, they established contact as they lunged. Legs I and, sometimes, open chelicerae and extended fangs of a lunging spider forcefully contacted the other spider at the end of the lunge. Judging from Laing's (1973) and our own (unpubl. data) observations, lunging during intraspecific interactions is similar, if not identical, to how *P. antipodiana* attacked large insect prey on its web. Occasionally, both spiders lunged simultaneously, but usually only one spider lunged at a time. Sometimes, spiders were grappling just before they lunged. Lunges were initiated by spiders close to, and often already in contact with, each other. During a lunge, the spider's palps were retracted.

Spiders might grapple immediately after lunging, or the two spiders might stand with legs intertwined for several seconds or minutes after a lunge, sometimes palpating intermittently but not grappling. The spider that was lunged at might immediately run away.

Sometimes a lunging spider's fang's punctured the other spider and caused injury or death.

Gape. A gaping spider held the basal segments of its chelicerae apart, with or without fangs extended.

Gaping display. While performing the gaping display, a spider gaped while holding its palps and cephalothorax raised high, usually with legs I and II elevated and extended forward. Drops of venom were often visible on the extended fangs (Fig. 11).

Spin. Spiders spun by sweeping their abdomens side to side, laying strands of silk across the web. The spider typically positioned the abdomen to the left or right, then swept it side to side (2–4 mm, 1–2/s) two or more times. Next the abdomen was returned into alignment with the cephalothorax or moved to the opposite side and swept from there. Spiders often walked slowly while spinning.

Clasp. Legs I of males (Fig. 12, 13), but not those of females and juveniles, have special structures ("claspers") which are used to hold on to ("clasp") other spiders. A clasper (Fig. 13) is an enlarged tibia and a strongly curved metatarsus.

A male extended one or both legs I forward (Fig. 12, 13) and, as a clasper contacted an appendage (Fig. 14, 15) of the other spider, the male flexed the tibia-metatarsus joint so that the clasper closed tightly down against the other spider's appendage and secured it tightly (Fig. 16). Pairs never separated until a male released his clasp on the female by extending his leg I tibia-metatarsus joints. A male usually clasped the female in a

Fig. 10 *P. antipodiana* female (left) lunges out of tunnel toward male approaching on right.



Fig. 11 *P. antipodiana* female in gaping display. Head-on view. Palps and legs I raised. Fangs extended. Venom drop visible on spider's left fang.

particular way before copulating (the copulatory clasp): the male placed his claspers over the basal-medial region of the female's two palps (Fig. 17, 18) and his tarsi I lay alongside the female's carapace.

Passive state. Clasped females became quiescent more or less immediately, except that they might slowly relax their chelicerae and let them close, this sometimes taking as long as 20 s. Also, females sometimes slowly repositioned their legs during the first minute after being clasped. The female subsequently entered a "passive state" (Fig. 18) by becoming completely quiescent and limp. A male might pull and push a passive female about, but she did not actively move herself.

On six occasions, we used a brush to force males away from passive females. These females remained in a passive state for about 5 min longer. During this time, they did not respond to us pushing them around with a brush or lifting them up with forceps.

Nip. Soon after the female became passive, the male nipped: while clasping the female, the male flexed legs I and brought his gaping chelicerae (but with his fangs retracted) against the ventral surface of the female's body. The male contacted the female's ventral cephalothorax or, occasionally, her abdomen. While pressed against the female, a male nipped by slowly opening and closing his gaping chelicerae (Fig. 19, 20).

Copulation. Before copulation began, the female always entered the passive state, after which the male pushed and pulled her into the copulatory posture. In this posture, the male's cephalothorax was about perpendicular to the ventral surface of the female's cephalothorax (Fig. 21, 22). The female's abdomen was often deflected ventrally or dorsally by as much as 45° (Fig. 21), and occasionally by as much as 90° from her cephalothorax.

Females copulating on the surface of a web sometimes lay on their backs (Fig. 23): the dorsal surface of female's abdomen on silk and cephalothorax angled from the web and abdomen by 45–90° (i.e., cephalothorax flexed ventrally with respect to abdomen). The male stood over the female, sometimes with his legs III and IV extended widely to the side and his abdomen angled down 45–90° from his cephalothorax. Spiders occasionally mated while lying on their sides on the surface of the web, but still in the typical copulatory posture.

Fig. 12 *P. antipodiana* male (right) turns toward female and extends leg I toward female (left). Note claspers on male's legs I but not on female's legs I.



Fig. 13 Pair of *P. antipodiana* males. Male on left extends legs I toward other male. Note claspers on legs I.



A copulating male usually held his face a few millimetres away from the female's sternum (Fig. 2). He brought his face into contact with the female for variable periods intermittently while copulating. Both sexes usually kept chelicerae closed while copulating. Both before and during copulation, the male sometimes drooled when his face was in contact with the female: fluid accumulated around the male's mouth and sometimes spread onto the female.

When spiders mated inside tunnels, the same copulatory posture was adopted as on the surface of the web. As the male pushed and pulled the female

into the copulatory posture, however, the surrounding silk was usually torn and the tunnel was enlarged or destroyed.

A male copulated by engaging one palp at a time, always keeping the unengaged palp close to the engaged palp (Fig. 22). While copulating, a male rotated his palps intermittently. When rotating, the two palps moved simultaneously, the right one clockwise and the left one anticlockwise, with tarsi remaining in place so that patellae traced crude circles with diameters of 1–3 mm. Legs and abdomen twitched almost imperceptibly while



Fig. 14 Pair of *P. antipodiana* males. Male in front begins to clasp other male with his left leg I. Clasper over patella-tibia of other spider's right leg II.



Fig. 16 Copulating *P. antipodiana* male (left) clasps female's two palps. Male's body about perpendicular to female's. Female (right) in passive state.

palps rotated, but at no other time. Observing details of copulation proved to be very difficult, but apparently each palp engagement was for only a few seconds.

End of copulation. Copulation always ended with the male disengaging while the female was still passive. After disengaging, the male always continued to clasp the female for a few seconds or,



Fig. 15 *P. antipodiana* male (left) begins to clasp female (right). Female, in passive state, pushed up and tilted over backward. Male's clasper on left leg I moving over female's right palp. Male's right clasper already clasps female's left palp.



Fig. 17 *P. antipodiana* female in passive state being clasped by male. Male's claspers over female's palps. Male's body obscured from view by female's body. Female's dorsal body surface in view. Female's body tilted up, her cephalothorax flexed back from abdomen. Female's fangs retracted.

occasionally, for as long as 1–2 min. Next he flexed legs I to pull the female closer, then pressed his face against her sternum and occasionally nipped the female briefly before releasing her. Release was always achieved by the male extending legs I fully to push the female far away (Fig. 24). Once released, the female remained passive for several seconds or minutes longer.

In one instance, a male stopped copulating, but continued to clasp the female's palps. The male groomed his palps for c. 6 min, while standing over



Fig. 18 Copulating pair of *P. antipodiana*. Viewed more or less side-on. Male (left) clasps female's palps. Female's body tilted up. Male's body about perpendicular to female's. Female (right) in passive state.



Fig. 20 *P. antipodiana* male continuing to nip (see Fig. 18). Chelicerae moving farther apart.



Fig. 19 *P. antipodiana* male (in front, dorsal body surface in view) nips female. Gaping chelicerae open and close while pressed against female's sternum. Chelicerae moving closer together in this photograph. Male clasps female aberrantly. Left clasper over female's palp tibia. Right clasper over female's leg II femur. Female's fangs retracted.

the passive female, then he flexed legs I, nipped the female, pushed her away, released his clasp and walked away. The female remained passive the whole time.

Aberrant clasping. Males sometimes clasped females aberrantly: clasper over only one palp, other leg I of male not clasping; one or both claspers over a femur or tibia of a leg I, II, or III of the female, one or neither of the female's palps being clasped at the same time (Fig. 19, 20, 25). Despite aberrant clasping, these females became passive. The male pushed and pulled the female about, sometimes eventually moving his claspers over the female's palps to establish a typical copulatory clasp. Usually the male began to copulate while maintaining the aberrant clasp.

Pairs never copulated, however, unless the male was able to align himself to a female in the typical copulatory posture. Occasionally, males clasping females aberrantly failed to establish this orientation



Fig. 21 Copulating *P. antipodiana* pair in typical posture. Bodies tilted up. Male's body (right) about perpendicular to female's body (left). Male clasps female's palps. Female in passive state. Female's abdomen flexed back from cephalothorax.



Fig. 22 Copulating pair of *P. antipodiana*. Male (below) with palps extended to female's ventral abdomen. Male about perpendicular to female. Female (above) in passivestate with body tilted up. Female's fangs retracted.

(Fig. 25); the female eventually came out of the passive state and the spiders separated.

While a male clasped her, the female usually held her palps raised, but more to the side than usual (tarsi sometimes angling out as much as 45°). If a male clasped her aberrantly, the female still held both of her palps in this configuration (Fig. 19, 20).

Twice, a male that clasped only one of a female's palps when copulation began had his free leg I passing between the spread apart basal segments of the female's chelicerae. The female's fangs were retracted. As the female slowly closed her chelicerae, the male removed his leg I and clasped the female's femur I.

Comparison of testing procedures

Spiders were more active when tested in reversed than in normal photoperiod, as reflected by more unsuccessful spontaneous encounters tests in normal than in reversed photoperiod (Table 2). In normal photoperiod, but not reversed, there were more unsuccessful tests in glass tanks than modular cages (Table 3).

There were fewer active interactions in forced encounters tests with escape ramps in place than without, in forced encounters tests in glass tanks than in plastic boxes with escape ramps, and in normal photoperiod rather than reversed in both forced and spontaneous encounters tests. In the

different types of pairings of spiders (male-female, male-male, and so forth), however, there were no evident differences in tendency to interact actively. Because there were no obvious differences in the details of the interaction in the different test setups, data were pooled.

There were long and frequent periods of inactivity during all types of tests. Activity, when it occurred intermittently, was often simply one spider walking briefly on the web. When one spider moved, the other sometimes rushed toward it, then both spiders froze; or one spider might chase the other before they froze. After brief bursts of activity, males often began to palpate.

Males sometimes alternated between chewing and palpating, especially if over a tunnel with a female inside: the male placed his fangs in the silk, chewed, removed his fangs, palpated, then repeated the sequence. Spiders never palpated while their fangs were penetrating the silk.

Spinning was a common behaviour of all sex-age classes in all types of pairings. It seemed to occur simply when spiders were activated. For



Fig. 23 Copulating pair of *P. antipodiana* on top of web. Male standing over female. Female lying on her back with cephalothorax tilted c. 45° up from web (i.e., ventral to abdomen). Aberrant clasp: male's left clasper over female's right palp tibia; right clasper over femur II. Female's fangs retracted.



Fig. 24 *P. antipodiana* male (below) ends copulation and moves away from female (above) by extending legs I. Note passive female is tilted up and her fangs are retracted. Male's palps hang loosely in front of chelicerae.



Fig. 25 *P. antipodiana* male (upside down, on left) perpendicular to female (right) establishes aberrant clasp. Clasper on male's right leg I goes over female's left femur I. Female became passive but pair did not mate.

example, when grappling spiders separated, they often spun as they moved away. One spider might lunge at another, after which the two spiders moved away and spun. After copulation males often walked away and spun, and females often spun after coming out of the passive state.

Males palpated in more tests of all types than did females and juveniles, and they palpated in more tests with females than in other types of pairings. Generally, if there was an interaction at all in a test that included a male, the male palpated.

Males always palpated before beginning to copulate and, with only three exceptions, before clasping the female. In one of the exceptional instances, a male that had not yet palpated clasped a female, then palpated (tarsi not touching the silk) briefly while he was clasping the female before



Fig. 26 *P. antipodiana* male (left) attempts to clasp female from rear. Female runs away into tunnel (right). Male's right leg I on female's abdomen.

starting to copulate. In the other two instances, a male clasped a female in her tunnel but could not push and pull her into the copulatory posture; he released her, backed out of the tunnel, then palpated for the first time; later, the female left the tunnel and the pair mated on the web.

Males usually started palpating before contacting the female. Sometimes, especially if the female was inactive, males contacted females before palpating. Generally, in male-female interactions, males palpated at a particularly fast and large amplitude, with the down motion distinctly faster than the upward return motion, so that the spider appeared to be forcefully pounding on the silk with its palps.

Male-female interactions

Early in an interaction, the female tended to stay in her tunnel and the male eventually came to spend more and more time on the web near, if not directly over, the tunnel (Fig. 6, 7). The male palpated much of the time. Sometimes, the female eventually came out of the tunnel, often by charging or lunging toward the male (Fig. 10). Alternatively, the male began to walk into the tunnel and the female rushed toward him.

After contacting a female, a male extended legs I and attempted to clasp her. The female sometimes foiled the male's efforts by moving rapidly away (Fig. 26). Female's often gaped when contacted by males, then grappled, lunged, or both. Males tended to gape when they contacted females.

Males occasionally entered tunnels, then clasped females and mated inside, but the female usually partially or completely left the tunnel before the

male clasped her and began mating. If a female was only partially out of the tunnel when she became passive, the male usually began to copulate with the female still partly in the tunnel (Fig. 27).

A female often lunged just before a male clasped her (Fig. 28). Males tended to be palpating when females lunged. As a female came lunging toward him, the male elevated legs I and angled them forward, bringing them into contact with the female to clasp her. Occasionally, a male's legs I were against the female but not clasping her, when the lunge ended.

If a female had been gaping, she began to close her chelicerae as soon as a male established a clasp. When a male extended legs I, but failed to establish a clasp on a lunging female, the female often continued to gape and sometimes repeatedly opened and closed her chelicerae slowly.

Once he was clasping a passive female, a male nipped then extended legs I to move his face 1–2 mm away from the female, after which he extended his palps and began to copulate. Males occasionally began copulating without first nipping. Instead, after a pause of a few seconds, a male simply extended his palps and began to copulate. In about half of these instances, a male brought his face to within a few millimetres of a female but made no contact with her. In other instances, a male contacted the female's ventral body with his face, with or without his chelicerae open.

One male extended legs I but failed to establish a clasp when a female lunged at him. The pair became quiescent with the female in the passive state. The male's femora I were against the female's palps and the distal parts of legs I lay on the female's carapace. Next, the male flexed legs I to bring his face against the female's sternum, after which he nipped then began to copulate. The male finally clasped the female's palps 20 s after starting to copulate.

Copulation duration was 27 ± 10.5 min (mean \pm SD) (range 12–69 min, $N = 51$).

Male-male, male-juvenile, female-female, female-juvenile, and juvenile-juvenile interactions

Males sometimes clasped juveniles and other males. Unlike females, males and juveniles remained active when clasped and generally attempted to back or walk away, sometimes pulling the clasping male across the web.

Males established a clasp on any segment of one or two of another male's or a juvenile's legs. The clasped spider's chelicerae often stayed open,

ften making biting motions. Unlike the biting motions of clasped females, those of males and juveniles were often rapid. A male might flex legs I and pull the other spider (a juvenile or another male) in, after which the two spiders often bit at each other and sometimes drew blood.

Sometimes two males clasped each other simultaneously. For example, when one male ran away, the other male might run after it and clasp one or both of its legs IV. One male might initiate a clasp when the other male lunged, or one male might clasp another male just after the two males

simultaneously lunged toward each other. Simultaneous lunges sometimes ended with each of the two males clasping the other. Males probed in all types of interactions, but probing behaviour appeared more forceful in male-male interactions than in other pairings.

Comments on palpating

In all types of interactions, palpating was usually preceded by contact (Table 8). Yet males, females, and juveniles all sometimes palpated before making contact with the other spider. Males were especially

Table 7 Behaviour of spiders just before first instance of palpating. Male-Female column: palpating by male; Female-Male, palpating by female; etc. Number: number of tests in which spider palpated.

	Male-Female	Male-Male	Male-Juvenile	Female-Male	Female-Female	Female-Juvenile	Juvenile-Male	Juvenile-Female	Juvenile-Juvenile
Clamber	139	95	36	13	9	1	3	2	23
Walking, pinning, ¹ No contact	14%	30%	0	0	0	0	0	0	17%
Chew, tug, ¹ tear silk, No contact	15%	6%	0	0	0	0	0	0	0
Chase, ² No contact	3-4%	3%	8%	0	22%	0	0	0	22%
Lunge, ³ No contact	0.5%	0	0	0	0	0	0	0	0
Probe, No contact	14%	0	0	0	0	0	0	0	0
Stab, ³ No contact	22%	0	0	0	11%	0	0	0	0
Contact then move apart	14%	15%	25%	15%	33%	0	0	0	0
Contact and chase ²	10%	20%	39%	23%	22%	100%	33%	50%	13%
Grapple then move apart, no gripping	15%	7%	8%	62%	11%	0	67%	50%	35%
Grapple, grip, then move apart	1%	3%	17%	0	0	0	0	0	0
Grapple then grip. Not move apart	8%	14%	0	0	0	0	0	0	0
Grip then move apart, no grappling	2%	0	11%	0	0	0	0	0	0
Grip. Not move apart. No gripping	0.5%	0	0	0	0	0	0	0	0
Lunge. Contact. move apart ³	11%	1%	17%	0	0	0	0	0	0

¹This behaviour performed by spider that palpated.
²Either spider chased the other, or the spiders alternated between chasing each other.
³This behaviour performed by other spider.

prone to palpate before making contact, especially in male-female interactions. Spiders sometimes contacted each other, then before palpating began, either one spider chased the other or the spiders just moved apart. Grappling was the most common preceding behaviour when females and juveniles palpated in interactions with males. Behaviour that preceded the male's first palpation, however, was highly variable.

Comparison of different types of interactions

There were four sex-specific behaviours (Table 7); only males clasped, nipped, and probed; only females became passive. Nipping and the passive state were seen only just before male-female pairs mated, and mating was never seen in the absence of these behaviours.

Males and females occasionally performed gaping displays during intraspecific interactions.

Table 8 Behaviour of spiders just before first instance of palpating. Male-Female column: palpating by male; Female-Male, palpating by female; etc. Number: number of tests in which spider palpated.

	Male-Female	Male-Male	Male-Juvenile	Female-Male	Female-Female	Female-Juvenile	Juvenile-Male	Juvenile-Female	Juvenile-Juvenile
Number	139	95	36	13	9	1	3	2	23
Walking, ¹ spinning.									
No contact	14%	30%	0	0	0	0	0	0	17%
Chew, tug, ¹ tear silk.									
No contact	15%	6%	0	0	0	0	0	0	0
Chase ²	3-4%	3%	8%	0	22%	0	0	0	22%
No contact									
Lunge. ³									
No contact	0.5%	0	0	0	0	0	0	0	0
Probe.									
No contact	14%	0	0	0	0	0	0	0	0
Stab ³									
No contact	22%	0	0	0	11%	0	0	0	0
Contact then move apart	14%	15%	25%	15%	33%	0	0	0	13%
Contact and chase ²	10%	20%	39%	23%	22%	100%	33%	50%	13%
Grapple then move apart.									
No gripping	15%	7%	8%	62%	11%	0	67%	50%	35%
Grapple, grip, then move apart	1%	3%	17%	0	0	0	0	0	0
Grapple then grip. Not move apart	8%	14%	0	0	0	0	0	0	0
Grip. Move apart. No grappling	2%	0	11%	0	0	0	0	0	0
Grip. Not move apart. No grappling	0.5%	0	0	0	0	0	0	0	0
Lunge. Contact.									
Move apart ³	11%	1%	17%	0	0	0	0	0	0

¹This behaviour performed by spider that palpated.

²Either spider chased the other, or the spiders alternated between chasing each other.

³This behaviour performed by other spider.

Fig. 27 Copulating pair of *P. antipodiana* at tunnel. Side view. Female (left) tilted up, with abdomen in tunnel. Male (right) about perpendicular to female. Male clasps passive female's palps.



Fig. 28 *P. antipodiana* female (left) lunges at male (right). Female's fangs extended. Male establishes aberrant clasp as female lunges (right clasper of male goes over female's femur I and left clasper goes over femur III). Female became passive; male moved his clasps to her palps.



Juveniles never did. All sex-age classes, however, could be induced to perform gaping displays if prodded forcefully in the face with a paint brush.

All sex-age classes chewed, tugged, and tore silk, but only males performed these behaviours frequently. Frequent tearing of silk by males was unique to male-female interactions. All sex-age classes grappled, lunged, spun, and stabbed, although stabbing was only infrequently seen. All sex-age classes palpated in all types of tests, but only males (in male-female and male-male

interactions) palpated frequently. Juveniles never killed or injured females. Otherwise, all sex-age classes at least occasionally killed or injured the other spider in all types of interactions.

Cannibalism

Only five females killed males (Table 9). Each time this was in a test during which she had not been clasped by the male. Two of these females ran over facing males before the males could raise legs I (Fig. 29). Three females chased down males from



Fig. 29 *P. antipodiana* female (above, left) feeds on male (below, right). Female killed male by running over him while he was facing her. Female's chelicerae over male's anterior dorsal abdomen.

behind. The two males attacked head-on and one of the three males chased down by the female had been palpating beforehand and had previously touched the female. The other two males were simply walking on the web and had not touched the female before being attacked.

Three males ran down and killed females without previously contacting or courting them (Table 9). On four occasions, however, a male first courted then killed a female (Table 9).

1. A male clasped a female's palps, then brought his face into contact with the passive female's sternum and nipped. While nipping, the male opened his fangs, bit the female, killed her, fed on her for c. 15 min, then released her and walked away.

2. A palpating male approached a facing female. When the male was 20 mm away, the female suddenly turned 180° and ran away. The male chased after her, bit her on the abdomen, killed her, fed on her for c. 30 min, then walked away.

3. A male contacted a female and she ran away, after which the male palpated briefly. When the female was walking in the web about 45 min later, the male chased her down and, killed her, and fed for over 2 h.

4. A male palpated and approached a facing female, then contacted her and began to grapple. While grappling, the spiders ended up venter to venter. The male inserted his fangs into the female's sternum, killed her, and fed on her for over 2 h.

Two males killed other males (Table 9). In one instance, the pair ended up venter to venter while grappling and the male on top inserted his fangs into the sternum of the other male. In the other instance, after a brief grappling bout, one male slowly moved his cephalothorax up and forward so that his chelicerae were over the other male's carapace. The male on top palpated for a few seconds (palps not contacting anything), while the other male remained quiescent. When the male below began to stir, the male above lowered his extended fangs to kill the other male. A similar sequence was observed once, but without cannibalism; this time, the lower male remained quiescent and the upper male palpated, then walked away, but did not lower his extended fangs.

Three males killed juveniles while grappling venter to venter, not having palpated beforehand. Another five juveniles were simply chased down and killed by males with no preliminary palpating or grappling. Still another male contacted a juvenile, palpated, then later, when the juvenile walked past, chased it down and killed it.

Two pairs of juveniles grappled briefly, separated, then grappled again. One spider of each pair palpated during the period of separation. The second grappling bout was longer, with the spiders ending up venter to venter. While venter to venter, one spider inserted its fangs into the sternum of the other. In one instance, the spider that had palpated previously was the victim; in the other, the palpatator was the killer. There were another two instances in which one juvenile killed another while grappling venter to venter, but there was no palpating these times. Another three juveniles simply ran down and killed other juveniles without previously contacting them (Table 9).

Juveniles never killed females, but two killed males while grappling (Table 9). In each instance, a juvenile slipped its cephalothorax over a male. One of these juveniles inserted its fangs into the male's carapace. The other inserted its fangs into the male's abdomen. Six females killed other females while grappling (venter to venter, 2; killer moved over carapace of victim, 4). No juveniles were killed by females while grappling. Instead, like seven of the instances of females killing other females, six juveniles were killed when females chased them down. Females never palpated in interactions in which cannibalism occurred.

In all tests in which one spider killed another, the killer ate the victim. Males might feed only briefly on females (see above); otherwise, the killer spider fed on its victim for several hours.

DISCUSSION

Gaping display

Laing (1975) described *P. antipodiana*'s gaping display in detail and provided evidence supporting the hypothesis that this is primarily an antipredator defence. He set up male-female, male-male, and male-female interactions (total of 100) but failed to see a full gaping display in any of these. Laing's laboratory observations of interactions between *P. antipodiana* and mice were of particular interest. He showed that, although mice will eat *P. antipodiana*, *P. antipodiana* is capable of defending itself by biting. The spider sometimes killed the mouse. Some mice retreated when bitten but did not die. When these mice were tested with *P. antipodiana* up to a week later, they retreated when the spider adopted the gaping display instead of approaching closely and attempting to kill the spider as they had done before. Unlike Laing (1975), we did see *P. antipodiana* adopt the gaping display during intraspecific interactions, but only rarely. Our observations are consistent with the gaping display being primarily an antipredator defence rather than a signal used in intraspecific communication. The gaping posture would seem to be significant in defence in at least two ways. A predator with good vision may be threatened by his posture, especially if it has had previous unpleasant experiences with *P. antipodiana*. Laing's study (1975) supports this hypothesis. *P.*

antipodiana's eyes are small and almost certainly incapable of acute vision, and it is not at all likely that *P. antipodiana*'s gaping posture is a visual deterrent to its predatory conspecifics. Whether the gaping posture might function as a threat display against predators with poor vision is unknown but difficult to envisage.

The other way in which the gaping posture might be significant in defence is by putting the spider in a position from which it can readily defend itself. With body raised and fangs open, the spider only has to lower its body rapidly to attack a potential predator that gets too close. Many predators, including conspecifics, would probably have difficulty subduing a *P. antipodiana* that has adopted the gaping display.

Our hypothesis is that the gaping display functions primarily as an antipredator defence. This display may sometimes be relevant to a *P. antipodiana* interacting with a conspecific, a conspecific being a potential predator. Similar gaping displays are also known for other spiders, including other mygalomorphs (Petrunkevitch 1911a, b). For most, if not all, of these species, gaping displays probably function primarily in antipredator defence.

The Australian funnel web spider, *Atrax*, performs gaping displays like *P. antipodiana*'s. *Atrax* backs up its antipredator threat display with a potent venom which is medically important and sometimes fatal to humans and other large animals (Sutherland 1972). *P. antipodiana*'s venom is not

Table 9 Behaviour of spiders in tests in which there was cannibalism. Male-Female column, male's behaviour; Female-male column, female's behaviour, etc. Number: number of tests in which there was cannibalism.

	Male-Female	Male-Male	Male-Juvenile	Female-Male	Female-Female	Female-Juvenile	Juvenile-Male	Juvenile-Female	Juvenile-Juvenile
Number	7	2	9	5	13	6	2	0	7
Spiders grappling	1	2	3	0	6	0	2	—	4
Killer ran down victim. No previous contact	1	0	1	2	1	4	0	—	3
Killer ran down victim. Previous contact	1	0	4	3	5	2	0	—	0
Killer gripping victim	1	0	0	0	0	0	0	—	0
Killer had palpated earlier	4	1	1	0	0	0	0	—	1
Victim had palpated earlier	0	0	0	3	0	0	0	—	1

especially potent against humans (Forster & Forster 1973), but *P. antipodiana* appears capable of backing up its threat display. *P. antipodiana*'s fangs are large and a bite is painful. Also, Laing (1975) showed that this spider's bite can be fatal to mice.

Clasping

Mygalomorphs seem generally to mate face to face, bodies tilted up, with the male extending his palps under the female (Foelix 1982), as described here for *P. antipodiana*. Mygalomorph males often have special structures on their forelegs which are known for some species to clasp the female during mating (Eberhard 1985). Although the anatomical details differ from species to species, we refer to all of these male structures simply as "claspers". The part of the female clasped also varies from species to species.

Comparative information about mygalomorph courtship and mating

Mating posture and clasping are the features of mygalomorph intraspecific interactions that have attracted the most comment. Some mygalomorph males clasp females' fangs when mating. When claspers are discussed in the absence of behavioural information, it is tempting to speculate that the male clasps the female's fangs. Todd (1945) and Forster & Forster (1973) suggested this for *P. antipodiana*, for instance. The prevalent interpretation of clasping has been that it is an adaptation of the male that functions to protect him from predatory conspecific females during mating. For example, Todd (1945) speculated that the male's claspers would clasp the female's open chelicerae and free the male from "the menace of the female's fangs" during copulation.

We will review what is known about intraspecific interactions of mygalomorphs, then consider the question of function. In particular, we will examine the question of how important cannibalism (females killing males) has been in the evolution of mygalomorph mating behaviour. There are four groups to consider: species which, like *P. antipodiana*, build sheet webs; trapdoor burrowing species; purse web spiders; and tarantulas.

Sheet web builders. Raven (1988) studied *Australothele jamiesoni* and provided unusually precise descriptions of courtship and mating. The male vibrated his body up and down and drummed with his palps as he approached the female. He raised legs I and made trembling movements with these

legs. The female raised her cephalothorax and forelegs when the male got close, and she partially extended her fangs. Eventually, the male pushed under the female. Males of this species have claspers on legs I and II. Legs I clasped the female's fangs. Legs II clasped the female's leg I tarsus-metatarsus joints. While establishing the clasp, the male drummed on the female's fangs with his palps.

Raven (1988) saw only one mating. Unfortunately, he accidentally bumped the cage while the pair copulated, whereupon the female impaled the male with her chelicerae. Interpreting what this observation implies about cannibalism is difficult at best. Raven suggested in his discussion that males are usually in little danger from females, yet he emphasised cannibalism in his introduction.

Hickman (1964) observed *Atrax infensus* mating. The male pushed the female up and appeared to push against her closed fangs with his legs I. There was no clasping. Pat Walker photographed a mating pair of *Atrax formidabilis* (fig. 21 in Scott 1980). The spiders were tilted up. The male's legs I crossed over at their metatarsi. Tarsi of these legs were against the female's closed fangs and between the female's spread apart chelicerae. Positioning of the male's legs was interpreted by Scott (1980) as the male pushing against the female's fangs to lock the "female's jaws apart so that she cannot strike at him".

Atrax formidabilis males have claspers on legs II that clasp the female's femora II during mating. Raven (1988) suggested that the male's behaviour of clasping the female with legs II was necessary to prevent the female from falling over backwards during mating. Whether the female becomes passive during mating was not made clear by Scott (1980), but this seems likely.

Snazell & Allison (1989) observed how *Macrothele calpeiana* (Walckenaer) mated. When the spiders contacted each other, the female reared up and extended her fangs, then the two spiders grappled with legs I and II. The female retracted her fangs almost immediately and the pair copulated. In the mating posture, tarsi and metatarsi of the male's legs I pressed against the sternum and closed fangs of the female. The male's tarsi and metatarsi II clasped the bases of the female's femora II. *M. calpeiana* males, having no claspers comparable to *P. antipodiana*'s, clasped females by simply flexing the tarsus-metatarsus joints of legs II. Once clasped, *M. calpeiana* females apparently became passive.

Bentzen (1975) studied courtship and mating of *Brachythele* spp. The male quivered his body when walking on the female's web. He touched the

male with his forelegs when he got close, whereupon the female raised legs I and opened her fangs. Males have claspers on their forelegs which were used to clasp the female's fangs. The female became passive as soon as the male clasped her.

Raven & Schwendinger (1989) observed *Hyxioschema suthepiae* mating. Using claspers on legs II, males clasped femora II of females and lifted females up into an upright position. Females mated at males as soon as males relaxed their claspers after mating.

Coyle (1985) observed the courtship and mating of *Microhexura montivaga* Crosby & Bishop. The male jerked his body up and down as he walked on the female's web. Sometimes the female reciprocated by jerking similarly. After contact, the pair grappled briefly, the female keeping her fangs extended. In the mating posture, the male used claspers on his tibia I to hold on to the female's palp femora. The female became passive.

Coyle (1986) observed the courtship and mating of *Euagrus* sp. The male "jerked-quivered" while on the female's web by moving his body up and down rapidly then vibrating his forelegs and palps. The female responded to the male by drumming her palps and legs I on the web. Eventually, when the male and female were close to each other and face to face, the male lunged at the female and, with his legs I and II, forced her up and back to assume the copulatory position with the female passive on her back and the male standing over her. The male used claspers on his leg II to hold on to the female's femora II. The female remained passive when the male finished mating and moved away. Coyle observed three matings, all in 47 × 25 mm vials. After one of these, the female came out of her passive state, moved about, located the male, and killed him within the confined space of the vial.

There are few reports on mygalomorph intra-specific interactions other than male-female. Paz (1988), however, observed web-defence behaviour by *Linothele* sp. but did not give details about behaviour.

Purse web spiders. Purse web spiders make a tightly-woven silk tube partly above ground and partly underground (Gertsch & Platnick 1980). The spider stabs through the silk with its fangs to catch prey that walk over the outside of the above-ground part of the tube (Bristowe 1958). There are numerous brief accounts of mating (Ennock 1885, 1892; Gerhardt 1929, 1933; Clark 1969; Coyle & Shear

1981). Males tear open silk tubes of females and go inside, then push under females to mate. Females are passive while mating.

Tarantulas. Petrunkevitch (1911b) observed the courtship and mating of *Dugesia hentzi*. Petrunkevitch (1934), Baerg (1928, 1958), and Hunt (1980) described similar courtship and mating in some other tarantula species. The male beat his forelegs on the ground and on the female, then moved around to face the female and touch her with his forelegs. When the female raised her body up and opened her fangs, the male used claspers on his legs I to clasp the female's fangs, then mated. Petrunkevitch said that clasping guarded the male against "possible injury or death from the female". Yet Petrunkevitch described the female as being "entirely disabled". The male pushed and pulled the female to position her properly for mating, the female apparently having become passive when clasped.

Minch (1979) observed courtship and mating behaviour of *Aphonopelma chalcodes* Chamberlin. A female emerged when a male tapped the top of her burrow. When the male touched her, the female reared up and extended her fangs. While vibrating his body up and down, the male tapped the female with his forelegs. The male used claspers on his tibiae I to hold on to the female's fangs while mating.

Trapdoor spiders. Buchli (1962, 1968) studied the courtship and mating behaviour of four species of trapdoor spiders (Ctenizidae): *Nemesia caementaris*, *N. dubia*, *Pachylomerus piceus*, and *Cteniza moggridgei*. Males palpated, tapped with their legs, scraped with their legs and palps, and pounded with their cephalothoraces on the ground around the trapdoor. If the female lifted the door, the male touched her legs and palps with his legs, his palps, or both. Males of the first three species clasped females' fangs, using claspers on legs I. *Cteniza* males, however, lack claspers and did not clasp females. *Amblycarenium* and *Ummidia* also lack claspers. Buchli (1968) noted that males of *Cteniza*, *Amblycarenium*, and *Ummidia* seem "more fearful of females" than do males in genera possessing claspers. Details concerning what is meant by "fearful" were not given, and no data are available for comparing frequency of cannibalism in the different genera.

Coyle (1971) observed the mating behaviour but not the courtship of *Atypoides riversi*. Males of this species have well-developed cheliceral

apophyses. Mating females kept their chelicerae open. The male positioned his chelicerae between the female's open chelicerae, seeming to apply considerable force to keep the female's chelicerae wedged open.

Passive state of female

It is clear that watching mygalomorph mating can create an expectation of great violence. Females often extend their fangs. Males grip the females' legs and palps, or even her chelicerae and fangs, before reaching under her to mate. The notion that a male is protecting himself from a *femme fatale* can be compelling.

But how real and immediate is the danger to a male? In particular, how often is a male really physically holding back an attack from a female? Interpreting clasping as a male's effort at physically restraining a predatory female is complicated by another apparently prevalent feature of mygalomorph mating—females of many species go into a passive state. In the passive state, which is sometimes called "catalepsy", a female goes limp and lets a male push and pull her around.

Porrhothele antipodiana females tended to lunge just before males clasped and lunging looks like predatory behaviour. It is tempting to argue that clasping functions to restrain a female at the moment of impact when she lunges, but this hypothesis does not explain why a male maintains a clasp after a female goes passive. Perhaps a male clasps a female as an additional (backup) protection in case she suddenly comes out of her passive state. *P. antipodiana* females, however, always came out of the passive state slowly, and we never saw a clasped female attempt to bite a male. The tendency to emphasise the potential of cannibalism and how a male may be physically restraining a female appears to divert discussion away from what may be more interesting communicatory functions of clasping.

The notion that a male's clasp physically restrains a lethal female just does not appear compatible with females being passive. It seems, instead, that a male's clasping behaviour provides a stimulus to which a female responds by going passive. This alternative to a hypothesis of simple physical restraint might still be compatible with the notion that males are protecting themselves from cannibalistic females, but the relationship between clasping behaviour, female passivity and the potential for cannibalism is unclear. Until this relationship is clearly explained, cannibalism cannot be said to "explain" the male's behaviour.

A communicative function may still be basically antipredatory. Clasping might provide a stimulus to which females respond by going passive, and a function of providing this stimulus may be to protect a male. This amounts to saying that, rather than physically restraining a cannibalistic female, a male "psychologically" restrains her. But why do female's respond as they do to this stimulus from males? Any explanation of passivity has to relate back to the female because passivity is, after all, a behaviour of the female: female passivity seems to imply the female's cooperation.

Porrhothele antipodiana females appeared ready to become passive when they lunged: the passive state was assumed very quickly once a male clasped a female. It is not as though females persisted in struggling and lunging at males only to be eventually subdued. Even when a male failed to clasp a female after a lunge, he was not injured by the female and, in one instance, the female went passive despite the male's failure to clasp her. Also, females went passive even when the clasp was aberrant, which is interesting because when the clasp was aberrant a female appeared free to move about and attack a male should she have tried to do so. "Female cooperation" does not mean anything like conscious decision making, of course. What we are suggesting is that there is an important, but perhaps easily overlooked, question about how becoming passive is adaptive for the female. This is, after all, a special behavioural response by females. Juveniles and males do not become passive when they are clasped.

Function of courtship

Is protecting the male from cannibalism an important function of courtship in spiders? Apparently, this hypothesis seems very compelling because, in one form or another, it comes up very frequently (e.g., Manning 1979; Uetz & Stratton 1983). Cloudsley-Thompson (1958) stated the rationale for this hypothesis especially eloquently: he referred to spiders as "inveterate cannibals" and pointed out that "it is obvious that mating is a hazardous undertaking fraught with danger, particularly to the male." The potential for violence and cannibalism seems to generate a special fascination in discussions of spider mating, making it almost disappointing (see comments by Starr 1988) when, after careful consideration, the anticannibalism hypothesis is not supported (see Jackson 1979, 1982; Jackson & Hallas 1986; Jackson & Pollard 1982).

This is not to say that sexual cannibalism is never important in the biology of any spiders (see Elgar &

ash 1988), but what about mygalomorph mating in aricular? Seeing these monsters among spiders mating, a female towering over a male with fangs extended, an impression of imminent violence is indeed strong. But does the cannibalism reduction hypothesis really help explain mygalomorph courtship in general and clasping behaviour in particular?

How often do female mygalomorphs actually kill, even attempt to kill, males? We did not see females direct much real violence at males in our study of *P. antipodiana*. *P. antipodiana* females are indeed cannibals. They did kill males, but in only five (2%) of the 211 male-female interactions observed.

Other researchers have seen mygalomorph males killing males, but we can also safely assume that, just about any time such violence is seen, an author will report it. We are more impressed by how few reports there actually are of females killing males, which is strange if cannibalism has really been so important in the evolution of these spiders' mating behaviour. In fact, some authors have commented on how peacefully male-female pairs of mygalomorphs live together in captivity (e.g., Hickman 1964).

Even a low frequency of cannibalism may be a significant problem for males, a problem solved by courtship. However, cannibalism was not a problem unique to *P. antipodiana* males during courtship. Courting males killed females about as often (four times) as females killed males! If significant cannibalism by females on males is implied by five incidents, then surely four incidents suggests significant cannibalism by courting males on females. How do females protect themselves against cannibalistic courting males! Does the female physically hold back the male? No. She becomes passive instead. A passive female cannot actively defend herself. Female passivity is troubling if we attempt to explain mygalomorph behaviour primarily in relation to protection against cannibalism, especially as a passive *P. antipodiana* female was killed in this study. This is not to say there are no arguments compatible with both female passivity and anti-cannibalism protection. For example, movement may be a primary stimulus that provokes predatory responses from males. Because a passive female removes these stimuli, she may gain protection when passive. Our goal is not so much to argue that cannibalism has had nothing to do with the evolution of mygalomorph behaviour but, instead, to argue that there is a need for critical examination of hypotheses about cannibalism.

Raven (1988) made an interesting suggestion about copulating pairs of *Atrax formidabilis* which should be considered in a broader perspective (see

Coyle 1971): a mating female *A. formidabilis* would probably fall over backwards if the male did not grip her and hold her upright. Males of this species gripped with legs II while legs I pushed against the female's chelicerae. Scott (1980) implied that leg I positioning was protecting the male from attack by the female and Raven did not dispute this explanation for leg I positioning.

If the posture of mygalomorphs generally tends to be with the female leaning up and if mygalomorph females often become passive while mating, then mygalomorph males may often need to hold females in position. Clasping a female's fangs, for example, may function in holding the female in place. It may also function in warding off attacks, but not necessarily. Just because fangs are weapons does not imply that a function of clasping fangs must be to ward off attacks.

Coyle (1971, 1985), one of the few authors not to emphasise cannibalism protection exclusively when discussing clasping behaviour, suggested that clasping behaviour of males provides signals to females. If clasping is a type of communication, then to what is this communication related? Reproductive isolation is one possibility (Coyle 1971). The hypothesis that courtship evolved as an isolating mechanism has held an important position in biology, yet supporting evidence in favour of this hypothesis is scarce for spiders and other animals (Hailmann 1977; Jackson 1982; but see Stratton & Uetz 1981). There is no obvious reason to expect the reproductive isolation hypothesis to be any more usefully applied to mygalomorphs than to most other spiders.

Coyle (1985) suggested that signals from male clasping behaviour may be significant in intersexual selection. He suggested that the female may be able to discriminate between male claspers of different geometry. If females prefer certain claspers geometries, regardless of whether such a preference is important in reproductive isolation, then female preferences may have been a selection pressure that influenced the evolution of the geometry of male claspers. It may also have been involved in the evolution of clasping behaviour because clasping is how males inform females about the geometry of their claspers. Eberhard (1985) made remarks similar to ours about mygalomorph claspers, and this hypothesis is analogous to Eberhard's (1985) hypothesis about the evolution of male genitalia.

Comparison of testing procedures

Many studies of the behaviour of spiders during intraspecific interactions have been laboratory-

based, supplemented by only a few, if any, observations from nature. For *P. antipodiana* and many (probably most) spider species, detailed studies based on spontaneously occurring interactions in nature would be impracticable. Yet this raises the question of whether observations in an artificial laboratory environment are representative of spiders' behaviour in nature.

Many species of jumping spiders (Salticidae) have been subjects of detailed laboratory-based studies of intraspecific interactions. However, when comparisons of laboratory-based and spontaneous field-based interactions have been possible (e.g., Jackson 1988), there has been no evidence of distortions of behaviour resulting from the laboratory environment. There is no obvious reason to expect mygalomorphs to be different from salticids in susceptibility to artefactual behaviour in the laboratory.

We never saw intraspecific interactions of *P. antipodiana* in nature. These interactions may occur only infrequently and, because *P. antipodiana* lives under stones, observations of intraspecific interactions in nature may be virtually impossible for most mygalomorphs. As an alternative, we observed *P. antipodiana* under a variety of laboratory conditions that varied in their similarity to the natural situation for this species. If observing interactions in the laboratory seriously distorts behaviour, then it seems likely that *P. antipodiana* would have behaved differently when tested under different conditions in the laboratory. Yet we observed the same basic behaviours regardless of testing methodology. The only clear difference concerned the ease with which interactions could be staged: more naturalistic methodology was less efficient for the researcher.

This does not prove that there are no serious laboratory artefacts. This study on *P. antipodiana*, however, plus previous studies on salticids, suggest that the onus is on the critic of laboratory studies of spider behaviour to demonstrate exactly how the laboratory might distort behaviour.

Display repertoire

Some of *P. antipodiana*'s behaviours appear to be intraspecific displays (i.e., behaviours specialised to function in communication between conspecifics: see Smith 1977). Having simple eyes, mygalomorphs almost certainly lack acute vision (see Land 1985). *P. antipodiana*'s displays probably provide tactile and chemotactic stimuli when the spiders are touching and web-borne vibratory stimuli when

the spiders are apart. We estimate that *P. antipodiana* has eight major displays (definition: Moynihan 1970): chew, grapple, clasp, nip, palpate, probe, stab, and tug. The traditional portrayal of mygalomorph display behaviour as "simple" (see Introduction) does not seem appropriate.

Chewing and tugging might give an initial impression of being primarily behaviours by which a male attempts to get through the silk and into the female's tunnel, but males did not actually use these behaviours to tear open tunnels. Tearing was achieved differently. Chewing and tugging appear, instead, to be important primarily as vibratory signals.

Grappling might appear to be simply an effort by two spiders to bite each other, but biting of large prey (both insects and conspecifics) was normally achieved at the end of a lunge. Grappling, being unique to intraspecific interactions and not being a routine preliminary to lunging, probably functions primarily as a tactile display.

Perhaps lunging during intraspecific interactions is also a display, even if it is very similar to how *P. antipodiana* lunges at large insects in typical predatory sequences. During intraspecific interactions, lunging only rarely ended in predation.

Stabbing, although it is a forceful movement of extended fangs toward another spider, was never a prelude to predation. This behaviour probably functions primarily in communication. The female's passive state appeared to be a stimulus to the male to mate, consistent with this behaviour being a display. Evidence in favour of interpreting clasping of the female by the male as being a display was discussed earlier. A communicatory function seems likely, regardless of whether or not this behaviour also has a role in physically restraining the female, positioning the female or both.

Perhaps spinning, being so prevalent in intraspecific interactions, is also a display. The spider's stepping gait might create distinctive vibrations or the silk may have pheromones associated with it. From other studies (Pollard & Jackson, unpubl. data), it is known that *P. antipodiana* uses pheromones during intraspecific interactions.

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Activity budget for breeding yellow-eyed penguins

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INTRODUCTION

The yellow-eyed penguin breeds along the south-east coast of New Zealand's South Island, on Stewart Island, and in the Auckland and Campbell Island groups (Richdale 1957). It is one of the largest bodied penguins breeding in the temperate zone (Stonehouse 1970), and may be found year-round in its breeding areas. Loss of natural breeding habitat and high chick mortality because of predation by introduced mammals are believed to have caused a significant decline in population levels (Darby & Seddon 1990). Despite the long-term studies of L. E. Richdale (1951, 1957) there is a lack of quantitative data concerning breeding behaviour of this penguin. This paper aims to quantify the time allocation of yellow-eyed penguins to the obligatory land-based activities of reproduction.

STUDY AREA AND METHODS

Observations were made at breeding areas on the Otago Peninsula, New Zealand. A variety of vegetation was present ranging from dense coastal scrub (e.g., *Hebe elliptica*, *Myoporum laetum*, *Urtica ferox*) to stands of flax (*Phormium tenax*), tussock (*Poa spp.*), and grazed pasture. Nests were on average 12-15 m apart and up to 350 m away from the sea.

Banding and marking

All the breeding birds in the two areas were individually marked with aluminium or stainless steel flipper bands. Six individuals were also fitted with a second flipper band bearing a colour code. This allowed individual identification of birds at up to 30 m distance. The sex of study birds was determined by one or more of a variety of methods: copulatory position (Seddon 1989a), chromosome analysis (Seddon 1988), skull morphometrics

Abstract Instantaneous scan sampling was used to determine time allocation for various breeding activities of the yellow-eyed penguin (*Megadyptes antipodes*), from pre-egg phase to post-guard phase. Breeding commences with the pre-egg phase, characterised by the presence of birds ashore during the day. Males are more active at this time, spending more time in an upright posture, preening, or displaying from the nest bowl. Females appear to follow an energy conserving strategy during egg deposition. Two eggs are laid, 3-5 days apart, with fully-prone incubation commencing after the laying of the second egg. Delayed onset of prone incubation is possibly because of low levels of egg predation and the temperate breeding climate. Incubation is shared by both sexes and, energetically speaking, is a period of hiatus; both birds gain weight during this time. Synchronous hatching caused by delayed incubation results in equal-sized siblings. Chick rearing is shared equally by both adults. The period of chick care is divided into the guard phase with one or other parent at the nest at all times, and the post-guard phase when both adults feed during the day.

(Darby & Seddon 1990), and behaviour during the pre-egg and laying phases (Richdale 1951).

Observations

Observations were made from hides during daylight hours (c. 0500–2100 h) over the 1985/86 breeding season, from the pre-egg phase in September 1985 through to the post-guard phase in February 1986. Five phases were identified:

- (1) pre-egg—from the time the adult birds first stay ashore during the day until the first egg is laid.
- (2) incubation—from the laying of the second egg to the hatching of that egg.
- (3) guard—period of 6–8 weeks after hatching when one or other adult remains at the nest.
- (4) post-guard—from the end of guard phase until fledging when both adults forage at sea during the day.
- (5) non-breeding—adults ashore during the day which are not associated with eggs or chicks.

Activity budgets were determined by instantaneous scan sampling at intervals of 1 min (Altmann 1974). Scans took between 1–5 s to complete. Observations were staggered so that all time periods were sampled. A total of 453 h of scan sampling produced 27 168 data points from observations on 20 individuals, comprising 19 breeding and 3 non-breeding birds (1 unpaired, 2 failed breeders) (Table 1).

Two categories of behaviour were recorded for each 1 min scan:

- (1) Posture
 - (a) Upright (Up) = body close to vertical.
 - (b) Prone (Pro) = body horizontal, breast on ground.
 - (c) Half-prone (HPro) = body between vertical and horizontal.
- (2) Activity
 - (a) Inactive (IA) = stationary, either resting/sleeping or awake.

(b) Comfort behaviour (CB) = including shaking, stretching, scratching, preening.

(c) Nest-building = construction and maintenance of the nest, including searching, collecting, carrying, depositing, and arranging nest material, scraping and mutual nest building.

(d) Sexual (SX) = associated with formation and maintenance of the pair bond, including mutual and allopreening, ecstatic and nest-relief displays (Seddon 1988), and copulation.

(e) Aggressive (AG) = agonistic behaviour.

(f) Parental (PR) = care of eggs or chicks, including egg-turning, chick-checking, preening, and feeding.

RESULTS

Posture

The changes in posture at the nest during breeding are given in Fig. 1. The percentage of time spent in each posture changed significantly between phases (Kruskal-Wallis ANOVA $P < 0.001$). Birds at the nest during the pre-egg phase were most often upright in the nest bowl. Following laying of the second egg, incubation proper commenced and a half-prone posture was commonest.

Guard phase was the most variable breeding phase. When the guard phase was divided into four quarters there was a clearer pattern of increasing time spent upright and decreasing time spent prone. Half-prone posture reached a peak in the second quarter (11–21 days) and decreased after that. By the third quarter (22–32 days) the chicks were no longer covered and the slight increase in prone posture in the fourth quarter reflects non-brooding resting by the guarding adult. Throughout the four quarters of the guard phase all postures changed significantly (Kruskal-Wallis ANOVA Up and Pro $P < 0.01$, HPro $P < 0.05$).

During this study, post-guard phase adults feeding chicks were ashore from late afternoon to early morning. During daylight hours an upright posture at the nest site was most common.

Activity

Activities at the nest changed during breeding (Fig. 2). Before laying, quiet inactive behaviour predominated with bouts of comfort behaviour, nest-building, and displaying. Incubating birds rested or sat quietly with only brief spells of comfort behaviour or nest-building. The amount of time spent in preening and other comfort behaviour and

Table 1 Sample sizes used for yellow-eyed penguin activity budget.

Phase	Number of individuals	Sex (M/F)	Number of minutes
Pre-egg	6	(3/3)	7929
Incubation	8	(5/3)	5536
Guard	15	(8/7)	10961
Post-guard	2	(1/1)	942
Non-breeding	3	(2/1)	1800
Total	20	(10/10)	27168

Fig. 1 Proportion of time spent (means and ranges) in upright (open bars), prone (cross-hatched bars), and half-prone (stippled bars) postures by yellow-eyed penguins.

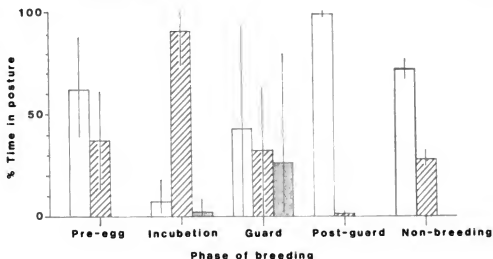
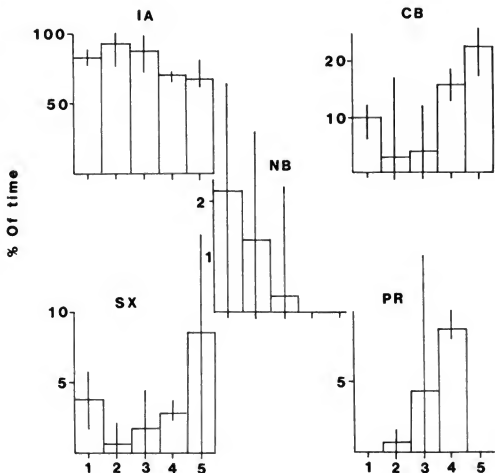


Fig. 2 Proportion of time spent in different behaviours (means and ranges) by yellow-eyed penguins. Phases: 1=pre-egg, 2=incubation, 3=guard, 4=post-guard, 5=non-breeding. Behaviours: IA=inactive, CB=comfort behaviour, NB=nest-building, SX=sexual, PR=parental.



parental care increased following hatching, whereas nest-building decreased.

When ashore, non-breeding birds preened and (when two birds were together) displayed more than breeding birds at any phase.

The relationship between posture and activity is given in Table 2.

Sexual differences

Overall, at the pre-egg phase males were significantly more often in an upright posture (Mann-Whitney U-

test, $P < 0.05$), and spent more time in comfort behaviour ($P < 0.05$) and displaying ($P < 0.05$) than females. When together at the nest in the pre-egg phase pairs would mutual preen, mutual nest-build, and mutual display. During mutual behaviours there were no significant differences in the amount of time spent upright. Full Trumpet (Richdale 1951) or Ecstatic (Seddon 1988) calls were given by lone males most frequently at dusk. With increasing nest density there was a greater frequency of vocal displays by individual males ($\chi^2 = 22.1$, d.f.=1, $P < 0.001$).

After laying, sexual displays were restricted to the mutual displays of nest relief. There was no difference between males and females in the amount of time spent prone on the clutch, though males spent more time in comfort behaviours (Mann-Whitney U-test, $P < 0.01$) and less time nest-building ($P < 0.05$) than did females.

There was no difference between the guard or post-guard posture or activity of males and females.

Incubation intensity

Between the pre-egg phase and the commencement of incubation proper there was a transition in posture at the nest (Fig. 3). With the arrival of the first egg the amount of time spent prone increased. A half-prone posture was seen during shuffling, settling, nest-arranging, and egg-turning. The laying of the second egg was associated with a further increase in prone posture, reflecting high incubation intensity. Activity changes over the same period are less marked. Changes in both posture and activity throughout the course of incubation were not significant (Kruskal-Wallis ANOVA $P > 0.05$).

DISCUSSION

Breeding cycle

Yellow-eyed penguin breeding commences when adults start staying ashore during the day. Lone

males or pairs occupy sites on or close to previous years' nests, but nest occupation at this time is not continuous at first. Gradually, over 1 or 2 weeks, occupation becomes continuous. High inter-nest spacing, preference for nest sites in dense vegetation (Seddon & Davis 1989), and low numbers of birds in a breeding area means that competition for nest sites or mate access is rare. Breeding birds may continue to take regular foraging trips during the pre-egg phase without risk of losing either nest site or mate.

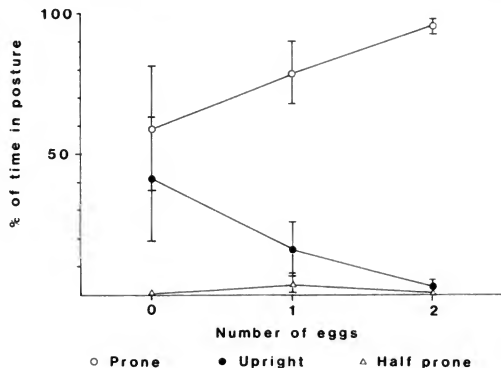
Richdale (1957) considered that, because of the continued association of birds with the breeding area throughout winter, by the commencement of the pre-egg phase most of the mated pairs for that season had been formed. Therefore, it is unlikely that initial male occupation of a site during the pre-egg phase is to attract a mate. This phase is a time of nest-selection, nest-building, copulation, and the reinforcement of the pair bond. The mutual displays of a pair coming together on a site and the mutual preening throughout the day have value in pair-bond reinforcement before incubation, when one or other bird will be absent from the nest during the day. Occupation and vocal display by males are part of the establishment of the nest territory, though active territory defence against conspecifics seldom occurs. Much of the mutual nest building occurring throughout the pre-egg phase probably also serves to reinforce the pair-bond.

Incubation proper begins up to 5 days after the laying of the second egg (Seddon 1989b). Between the laying of the first and second eggs, an interval of 3–5 days, the nest is usually occupied during the day by a lone female. As expected, the most marked behavioural change between the pre-egg and incubation phases is the increase in incubation intensity as indicated by time spent in a prone posture. The proportion of time spent prone by Adélie penguins (*Pygoscelis adeliae*) increases from 72% in the pre-egg phase to 87% during laying, with a maximum during incubation of 95%. The rapid build-up in incubation intensity by the Adélie penguin is thought to be necessitated by the harsh Antarctic environment (Derksen 1977). The temperate climate in which the yellow-eyed penguin breeds permits the increase in incubation intensity to be more gradual than that of the Adélie, with a more variable maximum. Low levels of egg predation (Darby & Seddon 1990) do not require the tight brooding of partially-completed clutches. The delay in the onset of a fully-prone posture results in synchronous hatching of siblings. The

Table 2 Percentage of time spent in different postures during activities by yellow-eyed penguins.

	Comfort		Nest-			
Phase	Inactive	behaviour	building	Sexual	Parental	Overall
Pre-egg						
Up	53.5	99.7	89.3	92.3	0.0	62.0
Pro	46.5	0.3	10.7	7.7	0.0	37.9
HPPro	0.0	0.0	0.0	0.0	0.0	0.0
Incubation						
Up	4.2	56.1	43.5	82.4	72.7	6.8
Pro	95.1	21.7	16.1	4.4	0.0	91.2
HPPro	0.7	22.2	40.3	13.2	27.3	1.9
Guard						
Up	43.0	61.0	51.2	84.6	55.0	42.5
Pro	34.1	5.7	2.4	6.7	1.4	31.6
HPPro	22.9	33.3	46.3	8.7	43.6	25.9
Post-guard						
Up	98.5	99.0	0.0	100	100	98.0
Pro	1.5	1.0	0.0	0.0	0.0	1.1
HPPro	0.0	0.0	0.0	0.0	0.0	0.0
Non-breeding						
Up	60.3	100	0.0	100	0.0	72.4
Pro	39.7	0.0	0.0	0.0	0.0	27.6
HPPro	0.0	0.0	0.0	0.0	0.0	0.0

Fig. 3 Proportion of time spent upright, prone, and half-prone (means and ranges) by yellow-eyed penguins, in relation to the number of eggs in the nest.



ability of pairs, in the absence of predation, to raise a full brood to fledging, and the low chick mortality caused by starvation suggest that yellow-eyed penguins rarely face unfavourable feeding conditions. It also suggests that food supply is normally reliable and abundant (but see van Heezik & Davis *in press*).

Guard phase commences as soon as the first chick clears its shell, and is characterised by the presence of one or other adult at the nest at all times. Changes in adult posture and behaviour during guard phase are related to the stimuli of two rapidly growing chicks. The most marked changes in adult posture occur between 21 and 32 days after hatching, when chicks start a period of rapid growth (van Heezik 1988) and develop homeothermy. The frequency of both prone and half-prone postures declines as the chicks are no longer covered. Increased chick mobility means that chicks spend less time in the nest bowl itself (Seddon 1990), with prone posture by the adult reflecting non-brooding resting on or near the nest bowl. The cause of the transition between guard and post-guard phases is not known. It is likely that an increased intensity of chick begging and the inability of one parent to feed two chicks combines with the breakdown of the nest site as a focus for feeding behaviour.

Sexual differences

Differences exist between the behaviour of males and females in the pre-egg and incubation phases. During the pre-egg phase males are more active

when ashore; they alone occupy the nest during the early stages, perform vocal displays, preen more, adopt a predominantly upright posture, and spend less time resting than females. During this time the female is using energy reserves in the production of the two-egg clutch. Time not spent feeding is passed in activities which conserve as much energy as possible. Burger (1981) hypothesised that males invest more towards territory and mate defence. The yellow-eyed penguin males' role in territory and mate defence is demonstrated by lone male nest occupation and display, and male presence with mates before laying. However, territorial disputes are rare because of the isolation of nest sites. Comparison of male and female behaviour on land indicates that males have built up greater reserves of energy by the start of incubation. He should thus be able to contribute more to incubation. Male yellow-eyed penguins generally take longer spells at the nest during incubation than do females (Seddon 1989b; but see Richdale 1951).

Energetically speaking, incubation in biparental breeders may be a "hiatus" period, allowing recovery from pre-egg activities (Byrkjedal 1985). Yellow-eyed penguin incubation is an inactive time spent largely resting in a prone posture. The main energetic burden is enforced fasting, though spells at the nest seldom exceed 5 days and are more often 1–2 days in length (Seddon 1989b). Increases in body weight over the incubation period (Richdale 1951) suggest that energy reserves may be stored in preparation for the more demanding phases of chick care to follow.

A detailed study of the energetic demands imposed by breeding, including an estimate of the energetic cost of foraging, is necessary to confirm the findings suggested by our results.

Further work is also needed to determine activity patterns of yellow-eyed penguins on land during the non-breeding phase. Yellow-eyed penguins are present in breeding areas all year round, often remaining overnight at or near old nest sites, and occasionally spending 1–3 days continuously ashore (pers. obs.). Yellow-eyed penguins may be particularly vulnerable to disturbance during the "re-occupation period" (Darby unpublished data) in early July when as many as 50% of the breeding birds in an area will start building and occupying nests. They then abandon these sites until the pre-egg phase in September. The importance for pair-bond formation or nest-site establishment of this and other land behaviours needs to be assessed.

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Relationship between invertebrates eaten by little spotted kiwi, *Apteryx owenii*, and their availability on Kapiti Island, New Zealand

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Abstract Invertebrates available to and those eaten by little spotted kiwi (*Apteryx owenii*) were studied in young and old forest on Kapiti Island from January 1984 to February 1985. Invertebrate availability was estimated by soil sampling, litter sampling, and pitfall trapping. Items eaten by kiwi were determined by faecal analysis and their contribution to the diet was assessed by numbers of individuals and biomass. Significantly more invertebrate food was available and arthropods eaten in the younger forest type. Little spotted kiwi are selective feeders, choosing large (body length ≥ 8 mm) slow-moving invertebrates from the upper layers of soil. Scarabaeid beetles and their larvae were the most commonly eaten arthropods. Little spotted kiwi feeding behaviour and diet was compared with that of weka (*Gallirallus australis*) on Kapiti Island; only minimal overlap was identified.

Keywords little spotted kiwi; *Apteryx owenii*; faecal analysis; feeding study; weka

INTRODUCTION

In pre-European times little spotted kiwi were widespread in both North and South Islands, but now survive in only one substantial population on one island: Kapiti Island ($40^{\circ}53'S$, $174^{\circ}55'E$). The species is endangered (Williams & Given 1981).

The conservation objective of little spotted kiwi management is to reduce the risk to the species by establishing viable populations on other islands. In order to assess the suitability of various offshore islands as liberation sites, knowledge of little spotted kiwi food and feeding behaviour is required.

Foods of little spotted kiwi are made up of a wide range of invertebrates and some vegetable matter, especially fruit (J. Jolly and R. Ordish, pers. comm.). Reid et al. (1982) suggested that kiwi may be random feeders and that numbers of prey ingested reflect supply rather than choice.

This paper presents information on the invertebrate foods of little spotted kiwi in relation to their availability. Our analysis was confined to invertebrates because they represent the most important component of the bird's diet. The diet of weka (*Gallirallus australis*) (Beauchamp 1987), a flightless rail of similar size to little spotted kiwi, is compared with that of *A. owenii*. Both species co-exist on Kapiti Island, at present in high densities (Jolly 1985, 1989).

Study sites

Kapiti Island lies 5.2 km offshore from Paraparaumu on the south-west coast of the North Island (Fig. 1). It is 9.6 km long, 2.2 km wide at its widest point, 500 m high, and has a steep western cliff line with the greatest part of the island sloping eastward into the sea.

Four sampling sites were chosen in two adjacent catchments on Kapiti Island: Te Kahu O terangi (Te Kahu) at 150-300 m a.s.l., and Te Rere at 300 m a.s.l. Young forest, modified by fires and grazing up until the 1920's occurs in the Te Kahu catchment, whereas older forest exists in Te Rere. All sample

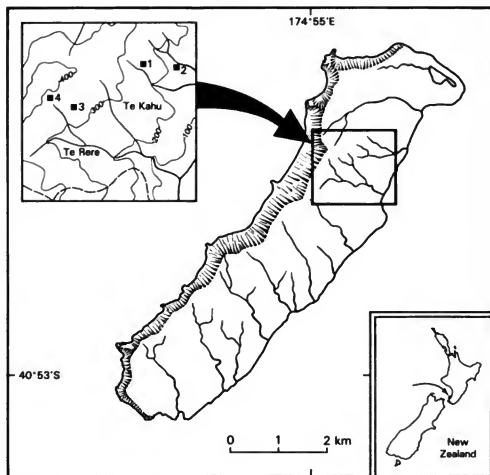


Fig. 1 Location of the four sites where invertebrates were sampled on Kaitiaki Island.

sites were on gentle slopes with an easterly aspect. In each catchment, one site was on a ridge and the other in a gully.

Forest canopy at site 1 on Te Kahu ridge comprised of kanuka (*Kunzea ericoides*), lancewood (*Pseudopanax crassifolius*), and kohuhu (*Pittosporum tenuifolium*) 12 m in height. A 4 m understorey consisted of mapou (*Myrsine australis*), rewarewa (*Knightsia excelsa*), kohuhu, heketara (*Olearia rani*), and kanono (*Coprosma grandifolia*). Beneath this, bare ground, kanono, hound's tongue fern (*Phymatosorus diversifolius*), and hook grass (*Uncinella* spp.) surrounded occasional seedlings of toro (*Myrsine salicina*), pigeonwood (*Hedycaria arborea*), and *Coprosma rhamnoides*.

Site 2, in the Te Kahu gully, was in a pure stand of 15 m high kanuka. A 10 m regenerating subcanopy dominated by mahoe (*Meliclytus ramiflorus*), but also containing fivefinger (*Pseudopanax arboreus*), kawakawa (*Macropiper excelsum*), heketara, and mapou, grew over a 2 m high understorey of nikau (*Rhopalostylis sapida*), kanono, kawakawa, kohekohe (*Dysoxylum spectabile*), and hangehange (*Geniostoma rupestre*). The ground was largely bare with some kawakawa, pigeonwood, kanono, nikau seedlings, and hen and chicken ferns (*Asplenium bulbiferum*).

At Site 3 on Te Rere ridge, the forest canopy was 20 m high tawa (*Beilschmiedia tawa*) with a sparse 4 m high understorey of pigeonwood and karamu (*Coprosma lucida*). At 1 m in height there were equal proportions of kanono, mapou, fivefinger, and horopito (*Pseudowintera axillaris*). Clumps of *Asplenium* spp, *Blechnum* spp, hound tongue fern, and filmy ferns (*Hymenophyllum* spp.) were scattered over largely bare ground.

At Site 4 in Te Rere gully, the 20 m high canopy was predominantly of tawa, with lesser quantities of mahoe and rewarewa. The subcanopy at 10 m consisted of kohekohe, kawakawa, and the tree fern *Cyathea smithii*, with some supplejack (*Ripogonum scandens*), heketara, and pate (*Schefflera digitata*). At 3 m the understorey was mostly pate with some supplejack and treefern. The ground was largely bare with occasional seedlings of kohekohe, kawakawa, and pate with *Blechnum* species, hen and chicken fern, and filmy ferns.

Average litter depth was 15 mm in Te Kahu and 35 mm in Te Rere. Soils in both areas were silty clays but those in Te Rere, particularly at Site 3, contained a greater organic fibre content than in Te Kahu. Soils at all sample sites became very hard in summer but very wet and soft after moderate rain.

The higher parts of Kapiti Island have a different climate from the rest of the island. The Te Kahu catchment has a similar climate to Paraparaumu Beach (the closest meteorological station where the mean daily temperature ranged from 9.8 to 17.2°C and annual rainfall was 930 mm during the study), whereas the higher Te Rere catchment was often in cloud and was damper. From August 1984 to February 1985 there was 12% more rain at Te Rere than at Paraparaumu Beach.

METHODS

Techniques used to sample invertebrates were based on those developed by Moed & Meads (1985, 1986, 1987). Three 10 m square grids were established at each of four sampling sites. Ten 20 cm square by 15 cm deep samples of soil were extracted randomly from the first grid and sorted for invertebrates on site. Five litter samples, each of 10 cm², were taken from the second grid and placed in calico bags. Invertebrates within these samples were later extracted using Tullgren funnels. At the third grid, 10 pitfall traps of the type and layout spaced 3 m apart in three rows) used by Moed & Meads (1985) were set for 1 month. Invertebrates were collected into Galis Solution.

Each site was sampled in April, September, and November 1984 and in February 1985. At the same time, little spotted kiwi faeces were gathered from and within the vicinity of burrows used by the birds within the catchments. Mandibles and other nutritious remains within faeces were compared to whole specimens of invertebrates for identification of prey and to give an indication of the minimum size of food items eaten by the bird. After determining the minimum size of kiwi prey (8 mm body length) invertebrates less than this length were discarded.

Except for earthworms, all invertebrate food items (numbers of individuals) recovered from kiwi faeces were counted. Estimation of absolute numbers of earthworms was impossible because only chaetae remained in the birds' droppings. Most worms cannot be identified from their chaetae and the number of chaetae per worm varies between species (Lee 1949). Seeds and large pieces of leaf fragments were recorded but identification of small ant fragments by their cuticle patterns was not attempted.

Since numbers of food items alone can give a false impression of an individual species importance

within the diet, mean biomass of each prey species was estimated. Biomass was determined as digestible dry weight. Dry weights were obtained by oven drying 5–10 individuals of a species simultaneously at 60°C until no further weight loss occurred. Individuals dried together were of different instars (which often varied greatly in size) collected throughout all four sampling periods. Numbers dried in each group were dependent upon numbers caught.

To determine digestible dry weight, individual groups of oven-dried invertebrates were immersed in concentrated hydrochloric acid for 8–10 h until the cuticle remaining was in a similar state to that found in the faeces of kiwis. These remains were then dried and weighed, digestible dry weight (biomass) being the difference between this value and the dry weight determined previously.

Relative biomass of each prey was estimated by using a correction factor (C.F.) obtained by dividing the biomass of each species group by the biomass of the largest taxon eaten, in this instance cicada (*Amphisalta cingulata*) nymphs.

Where appropriate, data (frequencies of occurrence of invertebrates, seasonal variation of invertebrate availability, and frequencies of invertebrates available and eaten) obtained from the two catchments were compared using χ^2 tests. Differences were regarded as significant if $P < 0.05$ unless otherwise stated. Seasonal comparisons of diet were not made because sample sizes were often too small.

RESULTS

Faecal analysis

Only the remains of invertebrates ≥ 8 mm body length were recovered from droppings of little spotted kiwi. At least 95% of the non-annelid invertebrates eaten were estimated to be less than 20 mm in body length. No ants, isopods, amphipods, bristletails, weevils, or large collembola were found in the faecal samples although these invertebrates were common in the litter.

More invertebrates were recovered per dropping in the Te Kahu catchment (mean 15.8 per dropping) than in Te Rere (mean 9.6 per dropping; Table 1). Furthermore, the mean biomass of invertebrates was higher in Te Kahu (0.9g per dropping) than in Te Rere (0.3g/dropping). Scarabaeid beetle larvae and adults occurred more frequently in faeces of little spotted kiwi from Te Kahu than from Te Rere

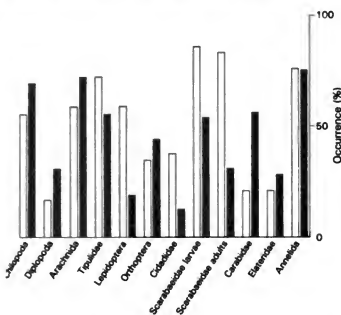


Fig. 2 Comparison between percentage occurrence of invertebrates found in little spotted kiwi faeces, over twelve months, in Te Kahu O terangi ($n = 29$; white bar) and Te Rere ($n = 32$; black bar), Kapiti Island.

larvae: $\chi^2 = 19.8$, d.f. = 4, $P < 0.01$; adults: $\chi^2 = 18.4$, d.f. = 3, $P < 0.01$). However, millipedes (Diplopoda), centipedes (Chilopoda), spiders (Arachnida), ranefly larvae (Tipulidae), and cicada nymphs (Cicadidae) occurred in faeces from the two catchments in similar frequencies. So too did earthworm chaetae (mean = 176 Te Kahu; 165 Te Rere).

The frequency of occurrence of invertebrates in 9 faeces from Te Kahu and 32 faeces from Te Rere is compared in Fig. 2. The relative biomass of invertebrates, excluding earthworms, in faeces from each catchment is shown in Fig. 3.

Compared to invertebrate remains, few plant remains were found in kiwi faeces. Five faeces from Te Kahu contained 11 seeds (8 five-finger and 3 lookgrass) and two faeces from Te Rere had 1 five-finger and 2 pigeonwood seeds. Also present were pieces of bark and intact leaf fragments of five-finger and ongaonga (*Urtica ferox*).

Food availability and relationship with food eaten

Collectively, more invertebrates were obtained from the two Te Kahu sites ($n = 1595$) than from those within Te Rere ($n = 1114$; $\chi^2 = 85.4$, d.f. = 1, $P < 0.01$; Fig. 4). Larger numbers of invertebrates occurred in the soil samples from Te Kahu than from Te Rere ($\chi^2 = 114.3$, $P < 0.01$) and in pitfall traps ($\chi^2 = 9.9$, $P < 0.01$), whereas similar numbers

of animals were present in the litter samples from the two catchments ($\chi^2 = 0.2$). The mean litter depth in Te Kahu, half that of Te Rere, meant invertebrates were collected from only half the volume of litter.

In Te Rere more invertebrates were obtained in soil samples from the gully than from the ridge ($\chi^2 = 48.7$, $P < 0.01$), and in Te Kahu, gully litter produced more invertebrates than ridge litter ($\chi^2 = 32.4$, $P < 0.01$). Similar numbers of invertebrates were caught in ridge and gully pitfall traps at both catchments.

The seasonal distribution of food items from the four sites is presented in Fig. 4.

The differences in frequencies of the various arthropods eaten and available varied considerably in both catchments (Te Kahu $\chi^2 = 2337.1$; Te Rere $\chi^2 = 2070.1$, d.f. = 12, $P < 0.01$; Fig. 5). Although centipedes were found throughout the year they occurred more frequently in autumn and winter (Te Kahu $\chi^2 = 25.3$; Te Rere $\chi^2 = 17.5$, d.f. = 3), mostly from the soil and litter samples (Fig. 4A). Similar numbers were obtained from both catchments. Centipedes collected were up to 70 mm in length, but most were 10–15 mm long and belonged to the slender burrowing Order Geophilomorpha. Generally, despite their abundance, centipedes comprised a small component of the diet in terms of numbers and biomass (Fig. 3, 5).

Millipedes were the most frequently recovered invertebrates from the soil samples in both catchments, especially in the gullies (Fig. 4B). They occurred least frequently in November and February in Te Kahu samples ($\chi^2 = 75.2$, d.f. = 3) and in February in Te Rere ($\chi^2 = 34.9$). In spite of their abundance they were eaten in small numbers (Fig. 2, 5).

Over twice as many spiders were collected from Te Kahu than from Te Rere (Fig. 4C). They were mainly true spiders from the litter and Mygalomorpha spiders (particularly Family Dipluridae) in soil samples and pitfall traps. They were available more frequently in summer in Te Kahu ($\chi^2 = 19.9$, d.f. = 3) whereas there was no seasonal difference in Te Rere. Most of the spiders in kiwi faeces were of the Mygalomorpha group. Spiders made up a greater component of the arthropods eaten in the Te Rere catchment than in the Te Kahu (Fig. 3, 5).

Moth larvae (Lepidoptera) of the family Geometridae were obtained mainly from litter samples and pitfall traps. They were uncommon in the Te Rere gully (Fig. 4D). Numbers declined significantly in summer (Te Kahu $\chi^2 = 34.3$; Te Rere

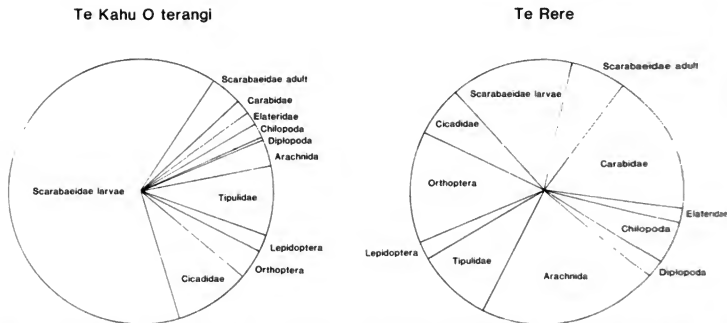


Fig. 3 Comparison between soft tissue (non-annelid) invertebrates biomass eaten by little spotted kiwis during the study in Te Kahu O terangi and Te Rere catchments, Kapiti Island.

$\chi^2 = 22.0$, d.f. = 3). Overall, low numbers of geometrid larvae were eaten (Fig. 3, 5) which may be because of their small mean size (8 mm length), since porina (*Trioxycanus enysii*) caterpillars (5 cm body length) were readily taken by little spotted kiwi living in grassed areas (J. Jolly and R. Ordish, pers. comm.). Adult geometrids were active in November and February and some were found in kiwi faeces then.

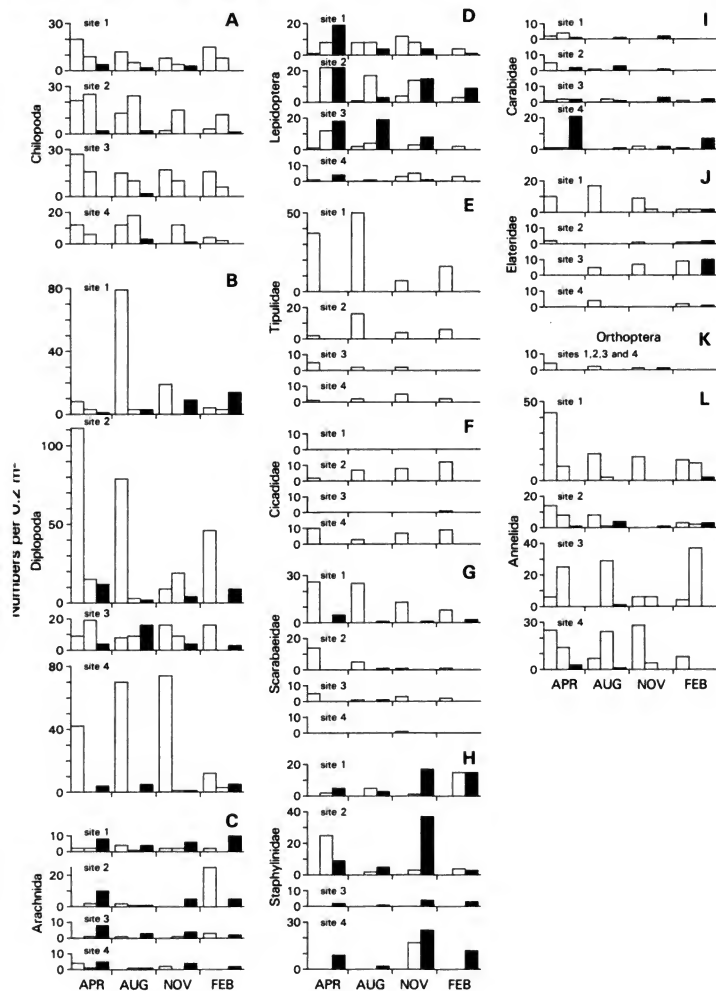
Crane fly larvae were collected only from soil samples and were particularly abundant at the Te Kahu ridge site (Fig. 4E). They were caught most often in autumn and winter in Te Kahu ($\chi^2 = 47.2$, d.f. = 3) but with no significant seasonal difference in Te Rere. Larvae tended to be clumped in the soil rather than scattered as individuals and were occasionally numerous in faeces (Table 1).

Cicada nymphs (*Amphisalta* spp.) were present in the gully soils throughout the year (Fig. 4F); however, there were significantly more in the Te Kahu samples in summer ($\chi^2 = 8.8$, d.f. = 3) but no seasonal differences in Te Rere. Most were found at a soil depth of 5–15 cm. Though not collected nor eaten in large numbers (Fig. 5), because of their large size they contributed about 10% of total arthropod biomass in both Te Kahu and Te Rere (Fig. 3).

Scarabaeidae larvae, particularly *Odontria piciceps*, *Costelytra* sp., and *Stethaspis longicornis*, were the most commonly collected coleopterans in soil sites. They were recorded most frequently at the Te Kahu ridge (Fig. 4G). Overall, larvae and adults were most available in autumn and winter in Te Kahu ($\chi^2 = 27.6$, d.f. = 3) but did not vary seasonally in Te Rere. Few larvae were present in soil samples in February whereas most adults were present in summer and autumn. Scarabaeidae larvae represented the most important non-annelid item of the kiwi diet in Te Kahu, and the second most important item, after spiders, in Te Rere (Fig. 3). However, eight times more larvae were found in soil samples from Te Kahu ($n = 92$) than from Te Rere ($n = 12$). Whereas adults were not as important as their larvae in the diet of kiwi, adult chafer beetles were seasonally important in February in Te Kahu and in April in Te Rere. These beetles usually become airborne at dusk, but return to the soil to lay eggs.

Staphylinid (Rove) beetle numbers peaked in November in both catchments (Te Kahu $\chi^2 = 23.5$; Te Rere $\chi^2 = 54.4$, d.f. = 3; Fig. 4H). No staphylinid beetles were found in kiwi faecal samples in spite of their being well represented in the litter (Fig. 5).

Fig. 4 Seasonal distribution in soil (shaded); litter (white); and pitfall traps (black); of: (A) Chilopoda; (B) Diplopoda; (C) Arachnida; (D) Lepidoptera; (E) Tipulidae; (F) Cicadidae; (G) Scarabaeidae; (H) Staphylinidae; (I) Carabidae; (J) Elateridae; (K) Orthoptera; and (L) Annelida at four sampling sites on Kapiti Island 1984–85. (Site 1 = Te Kahu ridge, Site 2 = Te Kahu gully, Site 3 = Te Rere ridge and Site 4 = Te Rere gully).



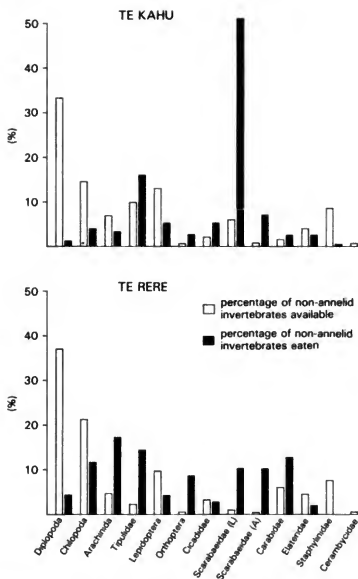


Fig. 5 Comparison between numbers of arthropods in little spotted kiwi droppings and numbers of arthropods ≥ 8 mm body length collected from litter, soil and pitfall traps at sampling sites in Te Kahu O terangi and Te Rere catchments, Kapiti Island.

Carabid beetles and their larvae were both most abundant in autumn (Te Kahu $\chi^2 = 20.2$; Te Rere $\chi^2 = 24.6$, d.f. = 3; Fig. 4I). Larvae were caught in soil and litter whereas adults were caught mainly in pitfall traps, especially at the Te Rere gully site. Adult Carabidae caught included: *Ctenognathus* sp., *Ilolaspis odentella*, *I. oedenema*, *Molopsida* sp., and the large species *Plecomostethus planiusculus*, *Zolus carinatus*, and *Z. femoralis*. The larger species of carabid beetle (10–20 mm) were eaten most often.

Similar numbers of Elateridae beetle and their larvae, mainly *Ctenicera* spp., were collected in Te Kahu and Te Rere (Fig. 4J). Most larvae occurred at the ridge sites in the higher levels of the soil and

occasionally in the litter. There was no seasonal variation throughout the year in Te Kahu. In Te Rere, Elateridae peaked in summer ($\chi^2 = 23.4$, d.f. = 3) largely through the presence of adults. Similar proportions of larvae and adults, relative to their availability, were found in faeces from the two catchments (Fig. 5).

The only weta (Orthoptera) recorded at sampling sites and within the faeces of kiwi was the ground-dwelling *Hemidrus furcifer*. Specimens of *H. furcifer* were recovered from soil samples in April and November (Fig. 4K). During summer, these wetas ascend from soil to trees (Moeed & Meads 1983) and two were caught in pitfall traps at that time. Most weta remains in kiwi faeces were collected during April and September (Table 1).

Earthworms make up 9.8% of all invertebrates collected from sample sites in Te Kahu and 20.5% in Te Rere. Earthworms were significantly more abundant in April in both catchments (Te Kahu $\chi^2 = 49.7$; Te Rere $\chi^2 = 9.0$, d.f. = 3; Fig. 4L). Most of the worms obtained from the soil were small (2–4 mm diameter), with some medium-sized specimens (4–6 mm diameter) and a few large species > 6 mm in diameter (*Octochaetis* spp.). Many worms from the litter were < 1 mm in diameter. The percentage occurrence of earthworms in the faeces (Fig. 2) from Te Kahu (76%) and Te Rere (75%) indicate they are an important item in the diet. Although we could determine preferences in the arthropod component of the diet (Fig. 5) we could not determine overall feeding preferences since we could not determine how much of the diet earthworms comprised. If the kiwi ate earthworms more often than expected by chance, other prey items would be less favoured. The converse would hold if kiwi ate earthworms less frequently by chance. To overcome this we tested the differences in the frequencies of the various invertebrates eaten and available with a range of hypothetical percentage values for earthworms eaten (Te Kahu; 9.8%, 30%, 50%. Te Rere; 20.5%, 30%, 50%). There were significant differences for each of the above values. (Te Kahu $\chi^2 = 2073.3$, 1862.6, 2835.4, respectively; Te Rere $\chi^2 = 1939.4$, 1585.6, 1394.6, respectively; d.f. = 11, $P < 0.01$).

DISCUSSION

Our results show that although invertebrates vary in abundance throughout a year there is always some food available to the birds in each catchment.

Overall, invertebrates were most abundant in the April and August samples (in particular millipedes, moth caterpillars, earthworms, carabid beetles, and in Te Kahu, tipulid and scarabaeid larvae). The first little spotted kiwi eggs of the season are laid in September (Jolly 1989). Abundance of food around September would not only be beneficial to the female developing her eggs but also to the male who has reduced feeding time while incubating from September onwards. Invertebrates whose abundance peaked in summer were spiders and icada nymphs in Te Kahu and elaterid beetles in Te Rere. Seasonal peaks in availability were more pronounced in Te Kahu, probably because of more extreme drying of soil in summer as a result of being below the cloud zone and the soil having a thinner protective litter layer.

Although a wide range of arthropods were recorded in little spotted kiwi faeces, some groups, in particular scarabaeid beetles, their larvae, and cranefly larvae, were recorded in greater numbers than their overall availability would suggest. The high percentage occurrence of earthworms in the faeces (Fig. 2) and their small contribution to overall numbers of invertebrates collected, particularly in Te Kahu (Fig. 4), strongly suggest that annelids were also selected for. Large, relatively immobile animals such as beetle larvae were preferred over small, active invertebrates like centipedes and millipedes. However, some large beetles capable of rapid movement, such as scarabaeids and carabids, were eaten. It is not known if kiwi are capable of digging these from the surface of the forest floor or not. Scarabaeid adults burrow into the soil for shelter and to lay eggs. While in the soil their mobility would be restricted. Similarly, carabid beetles shelter in crevices but not always out of the way of a robbing kiwi bill. Those invertebrate groups best represented in kiwi faeces were soil residents rather than litter or surface dwellers. These findings strongly indicate that little spotted kiwi are selective feeders, obtaining most of their food from the upper layers of soil. The evolution of a long thin bill with ostrils at the tip, would be advantageous for utilising this subterranean food source rather than for catching small active surface-dwelling prey. Average bill length for little spotted kiwi is 85.1 mm for females and 68.0 mm for males (Jolly 1989). The deep litter in Te Rere may restrict kiwi feeding to the uppermost soil levels. This may explain why more spiders were eaten there than in Te Kahu. Some invertebrates may have been avoided as food by little spotted kiwi, e.g., staphylinid beetles

and millipedes, two groups known to secrete defensive chemicals unpalatable to many predators (Barnes 1968; Richards & Davies 1977). Rove beetles, however, are known to be eaten by brown kiwi (*Apteryx australis*) (Watt 1971; Reid et al. 1982).

Two other large ground-dwelling species of insectivorous birds (weka and brown kiwi) co-exist with little spotted kiwi on Kapiti Island and could compete for food. A study of weka diet on Kapiti Island (Beauchamp 1987) revealed some overlap in its prey with that of little spotted kiwi. However, most prey items taken by weka tended to be smaller (>5 mm) and frequently included amphipoda, weevils, and small bush snails, items not taken by little spotted kiwi. Most of the invertebrates eaten by weka inhabited the litter or humus zones; these birds seldom grubbed into soil in search of prey and no remains of scarabaeid larvae were found in their faeces or gizzards. Fruit occurred in 18 of 20 weka gizzards. Average bill lengths for wekas on Kapiti Island were 47.1 mm for males and 43.9 mm for females. The differences in bill length of weka and kiwi, the dissimilarity of the food species they took, and their time of feeding (weka feed largely by day) probably result in there being little competition for food between the two species. Brown kiwi (of which there are 50–80 birds on Kapiti Island) often take the same food species as little spotted kiwi (Reid et al. 1982; Colbourne & Powlesland 1988). However, little spotted kiwi eat slightly smaller prey. Reid et al. (1982) found that most arthropods in 50 gizzards of North Island brown kiwi (*Apteryx australis mantelli*) were between 10–30 mm in length compared with our findings of 8–20 mm length in little spotted kiwi. Brown and little spotted kiwi may feed in different zones in the soils. With a proportionally stronger and longer bill (range 89.8–142.0 mm, $n = 62$ for adult North Island brown kiwi; Colbourne & Kleinpaste 1983), brown kiwi can extract invertebrates from almost twice the depth as little spotted kiwi. Smaller insectivores such as the robin (*Petroica australis*) and rats (*Rattus norvegicus* and *R. exulans*), which are abundant on Kapiti Island, may also compete for surface dwelling invertebrates, but their foods are unlikely to overlap with the soil component of kiwi diet.

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Diets of yellow-eyed, Fiordland crested, and little blue penguins breeding sympatrically on Codfish Island, New Zealand

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Abstract Diets of sympatrically breeding yellow-eyed (*Megadyptes antipodes*), fiordland crested *Eudyptes pachyrhynchus*, and little blue penguins *Eudyptula minor* were examined over 1 week in late October on Codfish Island, New Zealand to determine the degree of dietary overlap. Diets of yellow-eyed (YEP's) and fiordland crested (FCP's), and yellow-eyed and little blue penguins (LBP's) overlapped by 18% and 17%, respectively; LBP and FCP's by 46%. YEP's ate 7 species (out of a total of 16) that were not eaten by FCP's or LBP's, of which comprised 97% of the diet by weight, and 6 of which are demersal in habit. YEP's mainly ate fewer large individuals, whereas FCP's and BP's ate large numbers of small prey items. All species eaten by FCP's and LBP's were small juvenile forms that are found in the macroplankton, indicating foraging by FCP's and BP's was exclusively pelagic; YEP's foraged demersally as well as pelagically. This observation agrees with what is known of the foraging behaviour of mainland populations where sympatry does not occur.

Keywords: diet; yellow-eyed penguins; fiordland crested penguin; little blue penguin; little penguin

INTRODUCTION

On the mainland of New Zealand, yellow-eyed (*Megadyptes antipodes*) and fiordland crested (*Eudyptes pachyrhynchus*) penguins have allopatric breeding distributions. The former breed on the east coast of southern South Island and the latter on the west coast. Little blue penguins (*Eudyptula minor*) breed around most coastlines of New Zealand (Falla et al. 1981). Only on Codfish Island, situated off the north west coast of Stewart Island, do all three species breed sympatrically.

Egg laying of fiordland crested penguins (Warham 1974) begins 1-2 months earlier than for yellow-eyed penguins (Richdale 1957). Incubation and the guard stage of yellow-eyed penguins overlap with the chick-rearing phase of breeding fiordland crested penguins. Little blue penguins have a longer breeding season, which overlaps with that of both yellow-eyed and fiordland crested penguins, and sometimes includes a second clutch (Falla et al. 1981).

Foraging ranges are small for both fiordland crested penguins (<5 km) and yellow-eyed penguins (<15 km) on the South Island (van Heezik 1989, 1990). Little blue penguins are also inshore feeders in New Zealand (Gales 1984) and in Australia, where they forage mainly within about 10 km of their breeding colony during breeding (Gales et al. 1990).

Diets of yellow-eyed, fiordland crested, and little blue penguins at Codfish Island were examined during breeding to determine the extent of overlap in diet. General foraging behaviour may be extrapolated from diet composition to allow some comparisons between penguin species and between island and mainland populations to be made.

METHODS

Owing to limited opportunities for access to this closed reserve, Codfish Island (46°45'S, 167°40'E) was visited for only 1 week in late October 1984 when yellow-eyed penguins (YEP's) were

incubating eggs, fiordland crested penguins (FCP's) were feeding chicks, and little blue penguins (LBP's) were engaged in both of these activities. Stomach contents were obtained from 22 YEP's (12 adult, 10 juvenile), 21 adult FCP's, and 28 adult LBP's using the water flushing technique (Wilson 1984). Both adult and juvenile YEP's were flushed as numbers of YEP's were low. Two bays not more than 300 m apart were used as landing points by all three species; penguins were captured in these bays at dusk as they returned from foraging trips. A sample of the captured birds was weighed, and culmen length and gape (after Hulsman 1981) measured using Vernier calipers.

Excess fluid and loose flesh was decanted from the regurgitations. The remainder was preserved in alcohol and stored in sealed plastic bags. The entire regurgitation was sorted for otoliths, cephalopod beaks, and other diagnostic remains. Otoliths were identified, counted, and weighed, and allometric equations presented by Lalas (1983) were used to calculate total lengths and weights of fish consumed.

Cephalopod beaks were identified and their upper rostral length (URL)(squid beaks), or upper hood length (UHL) (octopus beaks) were measured. Weights of individual prey items were calculated from beak dimensions using the allometric equations of Lalas (1983). Equations were not available for all of the cephalopod species recovered. The equation for *Nototodarus sloanii* was also used for *Moroteuthis ingens*, both of which belong to the order Decembrachia. The equation for *Robsonella australis* was applied to *Octopus maorum* and

Ocythoe tuberculata, all of which belong to the family Octopodidae. The tiny size of most of the octopods and squid meant that potential errors from applying equations from other species were probably small, particularly in terms of their contribution to total mass. Beaks of *Nototodarus* were commonest in all three penguin species. Dorsal mantle lengths were measured from intact mantles. Any beaks too eroded or broken for URL measurement were probably from a previous foraging trip (van Heezik & Seddon 1989) and were not included.

RESULTS

Body weights and bill dimensions. Mean body masses and bill dimensions are shown in Table 1. Bill length was greatest in YEP's, intermediate in FCP's, and least in LBP's (Students *t*-test, $P < 0.001$).

Diet composition. Diet species are listed as percent contribution of calculated weight, percent of total numbers, numbers of individuals, and frequency of occurrence (Table 2). YEP's ate a greater variety of prey (16 taxa from 14 families), than the FCP (9 taxa from 7 families) and the LBP (7 taxa from 6 families). Number of taxa was unlikely to be a function of the number of stomachs sampled as the greatest number of samples were collected from LBP's, which ate the smallest number of taxa. Twelve of the YEP's sampled were juvenile birds (first year) and hence non-breeders. When only the diet of adults was calculated, the percentage contribution of the two main fish species increased whereas that of the other species, particularly squid, decreased. This trend was also observed in mainland populations (van Heezik 1990). There was no difference in number of species eaten by adult and juvenile YEP's.

Summed proportions of the five species common to all three penguins comprised 95% and 99% (by weight) of FCP and LBP samples, respectively, but only <3% of adult YEP diet (18% for all YEP's). Two prey species eaten only by YEP's (blue cod, *Paraperca colias*, and opalfish, *Hemerocoetes monopterygius*) made up 97% of the total calculated weight of adult diet (72% overall), but only 4% of total numbers. Hoki (*Macruronus novaezelandiae*) was only found in LBP and FCP samples, and sea perch (*Helicolenus percoides*), sprat (*Sprattus antipodum*), and the octopus (*Ocythoe tuberculata*) were only found in FCP and YEP samples.

Table 1 Bill dimensions and body weights of yellow-eyed (YEP), fiordland crested (FCP), and little blue penguins (LBP).

		YEP	FCP	LBP
body weight (kg)	\bar{x}	5.4	3.5	0.9
	SD	0.6	0.3	0.6
	<i>n</i>	20	20	28
bill length (mm)	\bar{x}	54.6	47.5	33.3
	SD	1.9	2.7	2.0
	<i>n</i>	21	21	12
gape (mm)	\bar{x}	33	33	24
	SD	1.9	1.9	1.9
	<i>n</i>	21	21	12
species/meal	\bar{x}	4.1	4.1	3.1
	SD	1.5	1.0	1.1
	<i>n</i>	22	20	26
	range	1-7	2-6	1-5

Squid weights were made up of *Nototodarus loanii* and *Moroteuthis ingens*, with *Nototodarus* comprising 93% (YEP), 96% (FCP), and 52% (LBP) of the total number of these cephalopods.

Using the index of percent similarity described by Brower & Zar (1977), diets of YEP's and FCP's, and YEP's and LBP's were found to overlap by only 18% and 17%, respectively. Diets of LBP's and FCP's overlapped by 46%.

Prey size. Size distributions of red cod (*Pseudophycis bachus*) and ahuru (*Auchenoceros punctatus*) differed between all three penguin species (Kolmogorov-Smirnov Test: red cod; $P < 0.001$; ahuru; $P < 0.001$) (Fig. 1A). FCP's took narrower distributions of both fish species; 80% of all red cod and 99% of all ahuru eaten were between 25–35 mm long. LBP's ate proportionately more smaller red cod than did YEP's or FCP's, although the range of sizes taken was similar to that of YEP's. LBP's ate a wider size range of ahuru than did FCP's, but did not eat ahuru >35 mm length, whereas YEP's ate ahuru up to 45 mm long.

YEP's ate more larger prey items. Blue cod (mean length = 169 mm, SD=67, $n=22$, range 60–298 mm) and opalfish (mean length = 107 mm, SD=61, $n=63$, range 30–310 mm) were species eaten only by YEP's, and were considerably larger than principal prey species in FCP and LBP diet. Fish <50 mm total length made up 100% of all fishes eaten by FCP's and LBP's and 96% by YEP's. However, in YEP's, the few individuals longer than 50 mm made up 82% of the calculated weight.

Weight distributions of squid eaten were not significantly different between YEP's and FCP's (Kolmogorov-Smirnov test, $P > 0.05$) and YEP's and LBP's (Kolmogorov-Smirnov test, $P > 0.05$), but differed between FCP's and LBP's (Kolmogorov-Smirnov test, $0.01 < P < 0.05$) with FCP's taking proportionately more from the smaller size classes. (Fig. 2) Squid weighing >50 g made up 29% of total squid weight in YEP diet, whereas all squid in FCP samples weighed <50 g, and <20 g in LBP samples.

Frequency of occurrence. Differences in prey size meant that species common to many samples were

Table 2 Diet of yellow-eyed (YEP), fiordland crested (FCP), and little blue (LBP) penguins at Codfish Island, showing % total calculated weight (% WT), % total numbers (% N), % frequency of occurrence (% FO), and total numbers of individuals (N).

Species		YEP					FCP					LBP				
		%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
		WT	WT	N	FO	N	WT	N	FO	N	WT	N	FO	N	WT	N
blue cod	<i>Parapercis colias</i>	77	57	1	50	21	–	–	–	–	–	–	–	–	–	–
opalfish	<i>Heimerocoetes</i> spp.	20	15	3	45	58	–	–	–	–	–	–	–	–	–	–
arrow squid	<i>Nototodarus sloanii</i>	<1	12	1	36	17	8	<1	80	73	58	2	57	77	–	–
warty squid	<i>Moroteuthopsis ingens</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ahuru	<i>Auchenoceros punctatus</i>	<1	4	86	100	1997	63	81	100	17418	37	88	89	1487	–	–
red cod	<i>Pseudophycis bachus</i>	<1	2	9	86	199	16	18	100	3804	1	6	75	97	–	–
sea perch	<i>Helicolenus percoides</i>	<1	4	<1	<1	2	5	<1	<1	2	–	–	–	–	–	–
sprat	<i>Sprattus antipodum</i>	<1	<1	<1	<1	1	<1	<1	<1	1	–	–	–	–	–	–
silversides	<i>Argentina elongata</i>	<1	<1	<1	<1	4	–	–	–	–	–	–	–	–	–	–
cockabully	<i>Trypterygion</i> spp.	<1	<1	<1	<1	3	–	–	–	–	–	–	–	–	–	–
hoki	<i>Macruronus novaezelandiae</i>	–	–	–	–	–	<1	<1	<1	26	<1	<1	25	16	–	–
sole	<i>Peltorhynchus latus</i>	–	<1	<1	<1	1	–	–	–	–	–	–	–	–	–	–
long-snouted	<i>Stigmatophora macropterygia</i>	<1	<1	<1	<1	2	–	–	–	–	–	–	–	–	–	–
pipefish	–	–	–	–	–	–	–	–	–	–	<1	<1	7	2	–	–
lantern fishes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
long-finned eel	<i>Anguilla dieffenbachii</i>	<1	4	<1	<1	1	–	–	–	–	–	–	–	–	–	–
octopus	<i>Octopus maorum</i>	<1	<1	<1	<1	10	8	1	80	291	3	1	11	13	–	–
	<i>Ocythoe tuberculata</i>	<1	<1	<1	<1	3	<1	<1	<1	5	–	–	–	–	–	–
errant polychaetes	–	<1	1	<1	<1	5	–	–	–	–	–	–	–	–	–	–

% WT* – percent weight of juvenile and adult YEP's.

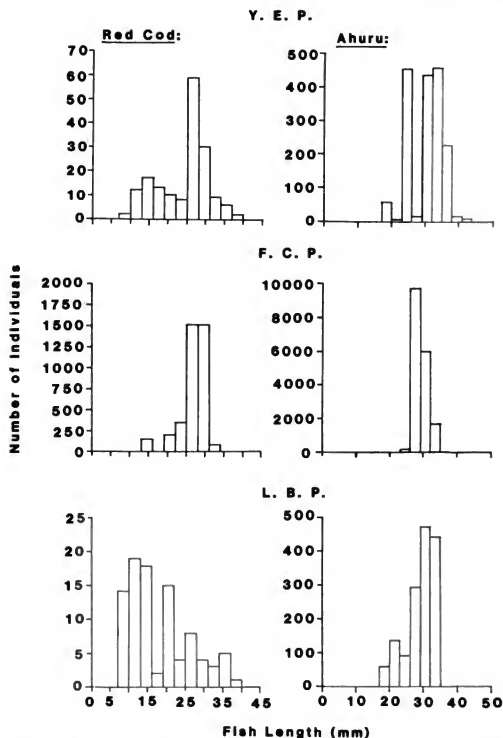


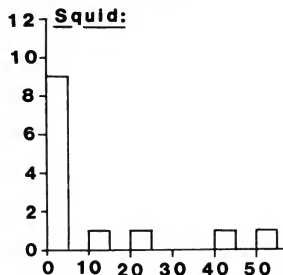
Fig. 1 Size-frequency distributions of red cod and ahuru in the diets of yellow-eyed (YEP), fiordland crested (FCP), and little blue penguins (LBP) penguins on Codfish Island, New Zealand.

not necessarily those that contributed largely to the bulk of the diet. Red cod was present in relatively large numbers in 86% of the samples collected from YEP's, 100% from FCP's and 75% from LBP's, but only contributed 2% to the diets of YEP's and LBP's, and 16% to FCP diet. Ahuru was also present in large numbers in all of the YEP samples, but contributed only <1% to the total calculated adult meal weights. Prey items such as sea perch and long-finned eel *Anguilla dieffenbachii*

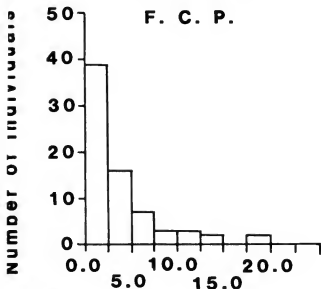
were only recorded once, but because of their large size they still made a discernable contribution to the total.

Variety of prey items. The mean number of different prey species per meal was the same for YEP's ($\bar{x} = 4.1$, $SD = 1.5$, range 1–7, $n = 22$) and FCP's ($\bar{x} = 4.1$, $SD = 1.0$, range 2–6, $n = 20$). LBP's ($\bar{x} = 3.1$, $SD = 1.1$, range 1–5, $n = 26$) took significantly fewer species during a foraging trip

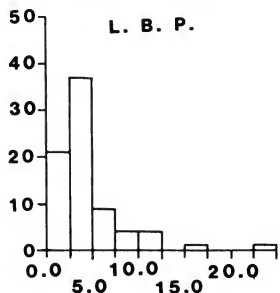
Y. E. P.



F. C. P.



L. B. P.



Mantle length (mm)

than either YEP's (Student's t -test $t = 2.660$, d.f. = 46, $P < 0.05$) or FCP's (Student's t -test $t = 3.178$, d.f. = 44, $P < 0.05$).

DISCUSSION

YEP's showed least overlap in diet composition because 7 out of the 16 species eaten by them were not taken at all by LBP's and FCP's, whereas LBP's only ate 1 species (lantern fishes) and FCP's ate none that were not found in diets of the other 2 penguins. YEP's ate a greater variety of prey, both in terms of number of species and prey size, the most significant difference being the consumption of adult blue cod and opalfish. These two species differ from other prey in that they are large and occur demersally, with blue cod common over rocky reefs and rock outcrops, whereas opalfish are found on muddy and sandy bottoms at depths from 5–200 m (Ayling & Cox 1984). Other typically benthic-dwelling species recovered from YEP samples, but absent from the diet of FCP's and LBP's, were polychaetes, sole, and cockabullics. Hence, YEP's appeared to spend a significant amount of time foraging demersally, whereas FCP's and LBP's foraged almost exclusively pelagically.

The tiny red cod, ahuru, hoki, arrow squid, warty squid, and octopus eaten by all three species of penguin are post-larval and juvenile forms, and are pelagic components of the macro-zooplankton (Habib 1973; Lallas 1983; Mattlin et al. 1985). Since it is unlikely that selection on the basis of preference is practised when such small items of prey are being swallowed from what are probably mixed-species associations in the macro-zooplankton, different size classes and proportions of cephalopods and the main fish species in LBP and FCP diet indicate that they were probably not feeding at the same feeding grounds.

Variations in diet composition between sympatrically breeding pygoscelid and eudyptid penguin species (in terms of prey size and species composition) have been attributed to different foraging ranges, life-history patterns and temporal patterns of food availability, rather than competition between penguin species (Trivelpiece et al. 1987; Adams & Brown 1989). Despite similarities in bill size and diving ability between FCP's and YEP's (at 3.5 kg FCP's are similar in body size to macaroni

g. 2 Size-frequency distributions of arrow squid in the diet of yellow-eyed (YEP), fiordland crested (FCP), and little blue (LBP) penguins on Codfish Island, New Zealand.

penguins *Eudyptes chrysolophus* which dive to depths of 10–100 m; Croxall et al. 1988), and maximum recorded dive depth of YEP's was 60 m (Seddon & van Heezik 1990). FCP's do not take the larger demersal prey species that are found in YEP diet. LBP's are also capable of diving to depths of up to 50 m (Gales et al. 1990), but their small bill size means they are unable to swallow larger prey items such as blue cod and opalfish. A more comprehensive study of FCP and YEP foraging is needed to understand why the observed foraging niche separation occurs.

FCP's on Codfish Island behave similarly to those breeding on the west coast of the South Island, where diet composition also indicated shallow dives and pelagic foraging (van Heezik 1989); Australian populations of LBP's have been shown to spend >75% of their time foraging within the top 5 m (Gales et al. 1990). Likewise, mainland populations of YEP's also spend some time foraging demersally, although at most localities proportionately more time is spent foraging pelagically on larger prey that are more available on the east coast (Ayling & Cox 1984; van Heezik 1990). YEP's may prefer larger prey items, which occur pelagically off the east coast of South Island (e.g., red cod, silversides, sprat; Ayling & Cox 1984), but forage demersally off Codfish Island where blue cod are known to be particularly abundant (Ayling & Cox 1984).

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Fruits, seeds, and flowers in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp/mixed hardwood forest, Orongorongo Valley, New Zealand

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INTRODUCTION

Abstract Seasonal and annual variations in fruits, seeds, and flowers eaten by possums in lowland podocarp/mixed hardwood forest, as revealed by faecal analysis, were recorded for 6 years (1978–83). Possums ate fleshy fruits of almost all such species available on the study area. Fruits of *Myrsine laevigata*, *Elaeocarpus dentatus*, *Nyctia excelsa*, *Macropiper excelsum*, *Melicope uniflorus*, *Pennantia corymbosa*, and *Urtica ferox* were eaten each year, and those of *Carpodetus fruticosus*, *Collospermum hastatum*, and *Passiflora vitifera* whenever they were available. Flowers of *Nyctia excelsa* and the introduced gorse, *Ulex europaeus*, also contributed substantially to their diet. Many other fruits, seeds, and flowers were eaten in small amounts.

Consumption of various fruit species was generally dependent on their availability in the forest, but a few species were preferentially browsed or avoided. Fluctuations in timing and intensity of flowering and fruiting were reflected in the amounts and seasonal occurrence of flowers and fruits eaten by possums. Possums also acted as both seed predators and seed dispersers. The partial placement of leaves in the diet by fruits was associated with the build up of body fat reserves in late summer and autumn.

Keywords Brushtail possum; *Trichosurus vulpecula*; diet; podocarp/mixed hardwood forest; fruit; flowers; seed predation; seed dispersal; annual variation; seasonal variation

The diet of the brushtail possum, *Trichosurus vulpecula*, in New Zealand native forests has been analysed in only five areas—the podocarp/mixed hardwood forest of the Orongorongo Valley, near Wellington (Mason 1958; Fitzgerald 1976, 1978); logged and unlogged areas of central North Island podocarp/hardwood forests at Pureora, Mapara, and Rotochu (Leathwick et al. 1983); forests in Waiho Valley and on Mt Bryan O'Lynn, Westland (Fitzgerald & Wardle 1979; Coleman et al. 1985); and remnant bush patches on Banks Peninsula, Canterbury (Gilmore 1966). Only Coleman et al. (1985) quantified the amounts of fruits eaten, although Mason (1958) and Fitzgerald (1976) noted that buds, flowers, and fruits were important foods, as had Kirk (1920) and Perham (1924) earlier. The importance of native fruits to possums is highlighted by significant correlations between the annual crop of hinau fruit (*Elaeocarpus dentatus*), which is eaten extensively by possums in March to July, and various measures of the reproduction and body weight of possums (Bell 1981).

Kean & Pracy (1953) and Pracy & Kean (1969) listed native fruits palatable to possums and commented that fruits were "of importance from midsummer until late autumn when they were almost of as much importance as leaves". They also discussed possible effects of possums on native birds through their consumption and wastage of fruit and flowers, particularly in poor or abnormal fruiting seasons. Recently, possums have been shown to eat a wide range of native fruits important in the diet of the North Island kokako (*Callaeas cinerea*); the effects of possums and other introduced browsing mammals on food availability in kokako habitats may partly explain the current decline in kokako populations (Leathwick et al. 1983).

The present paper reports the species and amounts of native fruits, seeds, and flowers eaten by possums in the Orongorongo Valley, and their seasonal and annual variation. Factors influencing selection of fruits by possums and energetic

considerations of frugivory by possums will be discussed elsewhere.

STUDY AREA

The study was carried out in podocarp/mixed hardwood forest adjacent to the junction of the true right bank of Wootton Stream with the Orongorongo River (41°22'S, 174°57'E; 18 km east of Wellington), about 3 km downstream from the DSIR Land Resources field station (Campbell 1984).

During the study (1978–84), the average annual rainfall at the field station was 2616 mm (range 1942–3424 mm), with a winter maximum. Mean maximum and minimum summer (December–February) temperatures were 21.1°C and 11.7°C, respectively. Winters were generally mild, with mean maximum and minimum temperatures of 11.6°C and 4.4°C, respectively. Occasional frosts occurred on the valley floor, but did not penetrate to the floor of the forest (Campbell 1984).

The study area was the site of a live-trapping grid for brushtail possums, with traps set at the intersections of 30 m squares over an area of about 8 ha. Traps were set for three consecutive nights each month from December 1977 to June 1984. Possums were uniquely identified by a combination of ear-tags and tattoos.

METHODS

Vegetation

The vegetation of the study area was surveyed in January 1981 to provide information on species composition and abundance, particularly for plants which produced fleshy fruits. Intersections of the possum trapping grid were used as the centres or end points of 33 plots, 20 × 4 m, randomly distributed over the area. Within each plot, the diameters at breast height (d.b.h.) of plants with d.b.h. >3 cm and the heights of plants between 1 m and 3 cm d.b.h. were measured. Epiphyte and liane species were recorded in eight 5 × 2 m subplots as few (<5), many (5–19), abundant (20 or more), or locally abundant (groups of 20 or more in a subplot). Botanical nomenclature follows Allan (1961) and Connor & Edgar (1987); information on growth forms and types of fruits was obtained from Allan (1961) and Moore & Edgar (1970).

Information on the timing of fruiting and flowering in Allan (1961) was supplemented with observations made during the routine monthly possum trappings. Data collected during 1980–85 on hinau flowering and fruiting (Cowan & Waddington 1990) also

provided information on flowering and fruiting of other species. In 1981 and 1983, fruit production of the same five karaka trees (*Corynocarpus laevigatus*) was estimated by counting fallen fruit on the ground at regular (usually weekly) intervals during the whole of the fruiting season.

Diet analysis

From January 1978 to June 1983 and from December 1983 to June 1984, one faecal pellet was collected from most possums on their first capture during each monthly trapping. Monthly sample sizes varied from 18–71 (mean \pm 95% C.L. = 42 \pm 4). Pellets were sieved individually (mesh size 355 μ m) in running water and then searched under a dissecting microscope at \times 10–40 for flesh and seeds of fruits and remains of flowers. These were identified by comparison with a reference collection.

All seeds of each species found in each faecal pellet were counted separately and, on occasions, a count was also made of broken seeds. If most seeds of a species were broken, numbers were estimated from counts of the larger remains. Flesh of fruits was generally only recorded as present, except for that of pigeonwood (*Hedycarya arborea*), matai (*Prumnopitys taxifolia*), and hinau, where quantities of flesh were estimated as few (0–5 pieces/pellet), medium (5–20 pieces), or common (>20 pieces); the estimates were converted to scores for analysis (few = 1; medium = 3; common = 5). Karaka flesh was not detected readily in possum faeces, so its importance was assessed directly by measuring possum browsing of the fruit flesh on fruits collected under karaka trees.

Flower remains were identified only for a few species. For some, only presence was noted, for others the number of stamens was counted; a few were recorded on the same few/medium/common scale as for flesh.

Percentage occurrence data were arcsine transformed for statistical analysis (Sokal & Rohlf 1981) or compared by χ^2 -tests on frequencies.

RESULTS

Vegetation

Twenty species of trees were recorded in the vegetation survey, 16 of which produced fleshy fruits (Table 1). However, 4 of the 16 did not fruit during the study. Fourteen shrub species were recorded, seven of which produced fleshy fruits, and all fruited during the study. Three of the seven lianes recorded (*Ripogonum scandens*, *Rubus*

Table 1 Total numbers of plants ≥ 1 m high recorded in the vegetation survey ($n = 33$ plots), percentage of plots containing each species, or at least 1 plant with d.b.h. > 8 cm, total basal area of plants with d.b.h. > 3 cm, and numbers of plants ha^{-1} by size class, 1–2 m high, 2 m–3 cm d.b.h., 4–8 cm d.b.h., > 8 cm d.b.h. [*Ripe fruit recorded on plants during the study. †Wholly or mainly dioecious.]

	Total plants	% Plots with			Plants ha ⁻¹			
		Species	Species >8 cm dbh	Basal area, m ²	1–2 m	2m–3 cm	4–8 cm	>8 cm
FLESHY FRUITED SPECIES								
Trees								
<i>Alectryon excelsus</i> †	64	39	3	0.117	159	38	19	27
<i>Aristotelia serrata</i> *†	6	9	3	0.011	0	15	4	4
<i>Beilschmiedia tawa</i>	2	6	6	0.090	0	0	0	8
<i>Carpodetus serratus</i> *	59	45	21	0.243	57	68	34	64
<i>Corynocarpus laevigatus</i> *	1	3	3	0.098	0	0	0	4
<i>Dacrycarpus dacrydioides</i>	3	6	0	–	8	4	0	0
<i>Elaeocarpus dentatus</i> *	7	21	6	0.698	49	4	4	8
<i>Hedycarya arborea</i> *†	245	85	45	1.426	447	182	170	129
<i>Melicytus ramiflorus</i> *†	169	82	73	6.522	83	19	152	386
<i>Myrsine australis</i> *	4	6	0	0.002	11	0	4	0
<i>Pennantia corymbosa</i> *†	913	100	42	1.047	1530	1375	409	144
<i>Podocarpus totara</i> *†	118	52	27	1.382	98	68	117	163
<i>Prumnopitys ferruginea</i> *†	23	33	3	0.012	61	19	4	4
<i>Prumnopitys taxifolia</i> *†	109	52	9	0.192	182	140	57	34
<i>Pseudopanax crassifolius</i> *†	21	24	6	0.024	45	23	4	8
<i>Streblus microphylla</i> †	7	15	0	0.001	8	15	4	0
Shrubs								
<i>Coprosma</i> (unidentified)*†	54	45	0	–	178	27	0	0
<i>Coprosma areolata</i> *†	380	91	3	0.033	735	625	76	4
<i>Coprosma grandifolia</i> *†	2	6	0	–	8	0	0	0
<i>Coprosma robusta</i> *†	1	3	0	–	0	4	0	0
<i>Macropiper excelsum</i> *†	701	79	6	0.187	1879	598	155	23
<i>Styphelia fasciculata</i> *	7	15	0	–	19	8	0	0
<i>Urtica ferox</i> *†	85	52	0	0.001	235	83	4	0
Vines								
<i>Ripogonum scandens</i> *	1	3	0	–	4	0	0	0
NON-FLESHY FRUITED SPECIES								
Trees								
<i>Knightia excelsa</i>	142	79	12	1.438	409	91	8	30
<i>Kunzea ericoides</i>	84	30	24	0.444	19	68	129	102
<i>Laurelia novae-zelandiae</i>	541	48	3	0.745	1208	769	68	4
<i>Pittosporum eugenioides</i>	2	3	0	–	8	0	0	0
Tree ferns								
<i>Cyathea dealbata</i>	3	6	0	–	8	4	0	0
<i>Dicksonia squarrosa</i>	1	3	0	–	4	0	0	0
Shrubs								
<i>Brachyglottis repanda</i>	14	15	0	–	34	19	0	0
<i>Buddleia davidii</i>	15	3	0	–	30	27	0	0
<i>Cassinia leptophylla</i>	4	9	0	0.003	4	4	8	0
<i>Geniostoma rupestre</i>	5	15	0	–	15	4	0	0
<i>Melicope simplex</i>	4	9	0	0.001	8	4	4	0
<i>Olearia rani</i>	8	9	3	0.029	11	8	8	4
<i>Ulex europaeus</i>	60	15	3	0.042	114	42	68	4
Others								
<i>Digitalis purpurea</i>	2	3	0	–	8	0	0	0
<i>Metrosideros diffusa</i>	1	3	0	–	4	0	0	0
<i>Pteridium esculentum</i>	1	3	0	–	0	4	0	0

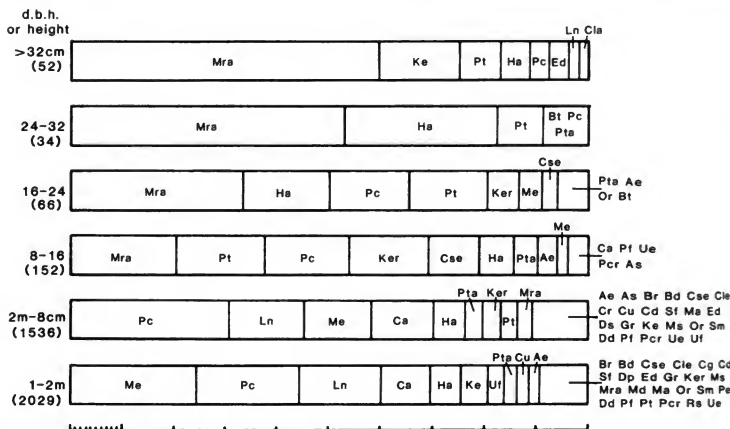


Fig. 1 Density distribution by size class of species of trees and shrubs recorded in the vegetation survey. Sample sizes in parentheses. Key for Fig. 1: Ae *Alectryon excelsus*; As *Aristotelia serrata*; Bd *Buddleia davidii*; Br *Brachyglottis repanda*; Bt *Beilschmiedia tawa*; Ca *Coprosma areolata*; Cd *Cyathea dealbata*; Cg *Coprosma grandifolia*; Cla *Corynocarpus laevigatus*; Cle *Cassinia leptophylla*; Cr *Coprosma robusta*; Cse *Carpodetus serratus*; Cu Unidentified *Coprosma* spp.; Dd *Dacrycarpus dacrydioides*; Dp *Digitalis purpurea*; Ds *Dicksonia squarrosa*; Ed *Elaeocarpus dentatus*; Glu *Griselinia lucida*; Gr *Geniostoma rupestre*; Ha *Hedycarya arborea*; Ke *Knightsia excelsa*; Ker *Kunzea ericoides*; Ln *Laurelia novae-zelandiae*; Ma *Myrsine australis*; Md *Metrosideros diffusa*; Me *Macropiper excelsum*; Mra *Melicotus ramiflorus*; Ms *Melicope simplex*; Or *Olearia rani*; Pc *Pennantia corymbosa*; Pcr *Pseudopanax crassifolius*; Pe *Periderium esculentum*; Pf *Prumnopitys ferruginea*; Pt *Podocarpus totara*; Pta *Prumnopitys taxifolia*; Rs *Ripogonum scandens*; Sf *Styphelia fasciculata*; Sm *Streblus microphylla*; Ue *Ulex europaeus*; Uf *Urtica ferox*

Table 2 Occurrence of epiphytes and lianes in the vegetation survey ($n = 33$ plots, 264 subplots).

Species	% occurrence		% abundance in subplots			
	plots	subplots	few	many	abundant	locally abundant
<i>Parsonsia heterophylla</i>	97.0	64.8	83.0	17.0	0	0
<i>Ripogonum scandens</i>	84.8	64.4	50.0	47.6	0	2.4
<i>Collospermum hastatum</i>	72.7	20.1	69.8	9.4	0	20.8
<i>Metrosideros diffusa</i>	63.6	32.2	45.9	21.2	8.2	24.7
<i>Griselinia lucida</i>	63.6	16.7	90.9	4.5	0	4.5
<i>Clematis paniculata</i>	42.4	11.0	96.6	3.4	0	0
<i>Passiflora tetrandia</i>	39.4	15.9	76.2	9.5	2.4	11.9
<i>Metrosideros perforata</i>	27.3	9.1	70.8	4.2	4.2	20.8
<i>Rubus cissoides</i>	15.2	3.1	87.5	12.5	0	0
<i>Astelia solandri</i>	9.1	1.5	100.0	0	0	0

ssoides, *Passiflora tetrandra*), the one shrub epiphyte (*Griselinia lucida*), and both perching liaceous epiphytes (*Astelia solandri* and *Collospermum hastatum*) produced fleshy fruits (Table 2). However, no fruit was seen on *Rubus* vines during the study.

Only eight species were represented among the largest of the trees (d.b.h. > 32 cm), and 88.5% were *M. ramiflorus*, *K. excelsa*, *P. totara*, and *H. arborea* (Fig. 1). Size classes d.b.h. 24–32 cm and 16–24 cm contained 6 and 11 species, respectively; 1% of trees with d.b.h. 24–32 cm were *M. ramiflorus*, *H. arborea*, and *P. totara*, and 86% of the smaller trees were the same three species and *P. corymbosa*. Fourteen species were in size class 8–16 cm d.b.h., with *M. ramiflorus*, *P. totara*, *P. corymbosa*, *H. arborea*, *K. ericoides*, and *C. serratus* together making up 85%. All trees with d.b.h. > 8 cm and which were common (>5% of size class) produced fleshy fruits or flowers which were eaten by possums, except *K. ericoides*.

M. excelsa, *P. corymbosa*, *L. novae-zelandiae*, *Prospira areolata*, and *H. arborea* contributed 56% and 75%, respectively of the shrubs and saplings 2 m high to 8 cm d.b.h., and 1–2 m high (Fig. 1).

In terms of basal area, the study area comprised mostly *M. ramiflorus*, *K. excelsa*, *H. arborea*, *P. totara*, *P. corymbosa*, *L. novae-zelandiae*, and *E. dentatus* (Table 1). About 82% of the total basal area of trees and shrubs with d.b.h. > 3 cm was fleshy fruited species. Individuals of fleshy fruited species with d.b.h. > 8 cm were much more common than those of species with “dry” fruits (983 vs 136 ha⁻¹; Table 1). Fleshy fruited plants were also dominant among the shrubs, with 1580 plants ha⁻¹ 1 m high to 3 cm d.b.h. compared with 196 plants ha⁻¹ for shrubs with “dry” fruits (Table 1).

Most of the fleshy fruited plants had short periods (< 3 months) of flower development, flowered in late spring and early summer, and had ripe fruit in late summer and autumn of the same year. A few species had prolonged flower development (> 6 months), notably *E. dentatus* and *K. excelsa*, or bore green fruit for 6–18 months before ripening, notably *C. serratus*, *H. arborea*, *P. taxifolia*, and *R. apida*.

Some plants were uncommon or had restricted distributions on the study area (Tables 1, 2), which probably affected their occurrence in the diet of possums. Introduced species in particular were confined largely to the stream and riverbank, and to the verges of a vehicle track which traversed the

study area. The native species *P. totara* and *K. ericoides* were also restricted largely to near the stream and riverbank.

Native flowers and fruits eaten by possums

Flowers were eaten by possums generally in late spring and early summer, though buds of some species which had prolonged flower development (e.g., hinau) were eaten over an extended period. Possums ate generally only the fruits of fleshy-fruited plants. Fruits of native plants were eaten in every month, but both variety and numbers were greatest in late summer and autumn (Table 3). The same flowers and fruits featured in the diet of possums each year, though their relative importance varied.

The following accounts of individual species briefly describe seasonal and annual variations in the occurrence and amounts of flowers, fruits, and seeds eaten by possums.

Carpodetus serratus (putaputaweta) (Fig. 2)

Putaputaweta flowered from late November to February. Fruit developed until the following year, when it ripened during February to August, but mostly in April and May, when most seeds were found in the litter cones. Putaputaweta fruits were eaten by possums only when ripe or nearly ripe, although green fruit was available for most of the year. The proportions of possums eating putaputaweta fruits during February to June varied significantly between years ($\chi^2 = 167.65$, $P < 0.001$). More seeds were eaten in 1978 than in either 1982 ($t = 3.09$, $P < 0.01$) or 1984 ($t = 2.63$, $P < 0.02$). In 1979–81 and in 1983 putaputaweta fruits were hardly eaten at all.

Collospermum hastatum (kokaha) (Fig. 3)

Kokaha flowered from late December to March, with a peak in late January and early February when inflorescences browsed by possums were occasionally found on the ground. Possums ate kokaha fruits in only 4 of the 7 years, and mostly between March and May. The proportion eating kokaha fruit between January and June was greater in 1979 and 1982 than in each of 1978 and 1981 ($P_s < 0.01$). More seeds were eaten in 1982 than in 1979 ($t = 2.36$, $P < 0.02$). The seeds of the other large perching liaceous epiphyte on the study area, *Astelia solandri*, were recorded only occasionally (March 1978, April and May 1982); *A. solandri* was much less common on the study area than *C. hastatum* (Table 2).

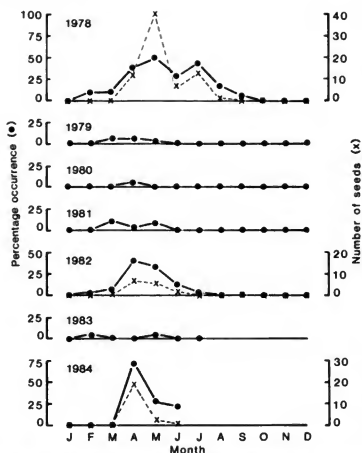


Fig. 2 Percentage occurrence and mean number of seeds of *Corypodetes serratus* fruit in possum faeces. Only a few seeds were found in 1979–81 and 1983.

Corynocarpus laevigatus (karaka) (Fig. 4)

Karaka flowered from October to December. Possums ate only the flesh from karaka fruits, and it was not readily identified in the faecal samples. Nor could feeding by rodents, birds, or possums be distinguished when all the flesh had been stripped from the fruit. However, 96% of 400 partly-eaten fruit examined in 1981 had possum incisor marks and 98% of 200 fruit examined in 1975 had been chewed by possums (M. J. Daniel, pers. comm.). Possums were therefore probably responsible for most feeding on karaka fruit.

Possums ate the flesh of most karaka fruits as soon as they ripened, mostly during February and March. During the 1981 and 1983 fruiting seasons, only 13.7% of 1844 fruits and 7.7% of 2291 fruits, respectively were intact when first found, and most of those (49.4% in 1981 and 48.9% in 1983) were green and unripe, with only 15.8% and 12.5%, respectively being fully ripe. Green fruit and the unripe parts of ripening fruit were rejected by possums; the flesh of only 3 out of 29 marked green fruit was eaten overnight compared with 18 out of 28 partly-ripe fruits ($\chi^2 = 15.6$, $P < 0.01$). On a different night, the flesh of only 7 out of 31 green fruit was eaten compared with that of 10 out of 10 wholly ripe fruit and 20 out of 26 partly-ripe fruit ($\chi^2 = 22.5$, $P < 0.01$).

Table 3 Periods of major feeding by possums on commonly eaten native and introduced fruits.

Species	Summer			Autumn			Winter			Spring		
	D	J	F	M	A	M	J	J	A	S	O	N
Native												
<i>Carpodetus serratus</i>					X	X	X					
<i>Collospermum hastatum</i>				X	X	X						
<i>Corynocarpus laevigatus</i>			X	X								
<i>Elaeocarpus dentatus</i>					X	X	X	X				
<i>Hedycarya arborea</i>	X	X	X									
<i>Knightia excelsa</i>					X	X	X	X				
<i>Macropiper excelsum</i>			X	X								
<i>Melicytus ramiflorus</i>		X	X	X	X							
<i>Passiflora tetrandra</i>					X	X	X					
<i>Pennantia corymbosa</i>			X	X	X							
<i>Prumnopitys taxifolia</i>				X	X	X	X					
<i>Urtica ferox</i>		X	X	X	X	X	X					
Introduced												
<i>Solanum nigrum</i>			X	X	X	X	X					
<i>Stellaria media</i>	X	X										X
<i>Polycarpon tetraphyllum</i>	X	X	X	X								
Total native	1	3	6	7	9	7	6	2	0	0	0	0
Total introduced	2	2	2	2	1	1	1	0	0	0	1	0
Total combined	3	5	8	9	10	8	7	2	0	0	0	1

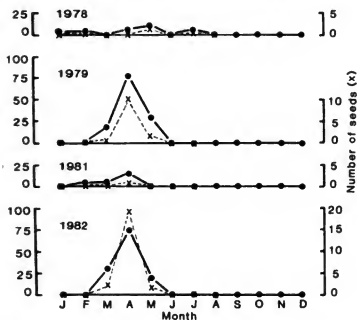


Fig. 3 Percentage occurrence and mean number of seeds of *Collospermum hastatum* in possum faeces. No seeds were found in 1980, 1983, or 1984.

Although ripe fruit fell from some trees for up to 30 days, at least 80% of the fruit of each tree fell over a period of only 30 days (Fig. 4). The amounts of fruit falling varied enormously from tree to tree and from year to year; trees did not produce large fruit crops in successive years (Table 4).

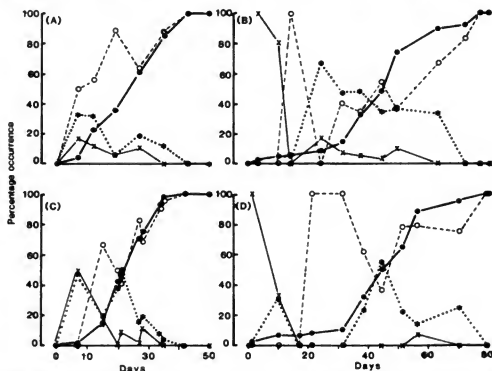


Fig. 4 Fruitfall under individual trees of *Corynocarpus laevis*. Tree 1: A = 1981, B = 1983. Tree 2: C = 1981, D = 1983. (x) percentage of green fruit; (*) percentage of partly eaten fruit; (○) percentage of wholly eaten fruit; (●) cumulative percentage of total fruitfall [$n = 136, 232, 546, 60$ for Tree 1 (1981, 1983) and Tree 2 (1981, 1983), respectively]. Samples were collected at various intervals after the first fruitfall.

Elaeocarpus dentatus (hinau) (Fig. 5)

Hinau flowered each year in November to January though flower buds were present from April onwards. Hinau flower stamens and anthers were found in possum faeces from September to February. Flower buds were also common in June to September, though their presence was not recorded systematically. The overall occurrence of flowers in the diet from October to January varied significantly between years ($\chi^2 = 12.73, P < 0.02$). It was greatest in 1978/79 and least in 1981/82.

No hinau seeds were found in possum faeces, only the remains of flesh and skin. Hinau fruit was eaten by possums from March to September, but most commonly in April to July. Percentage occurrence varied significantly between years ($F_{6,66} = 4.18, P < 0.01$), with occurrence in 1979 significantly greater than in all other years ($P_s < 0.01$). The mean score index of amount showed similar significant variation between years ($\chi^2 = 70.06, P < 0.001$), with the greatest amounts of hinau fruit eaten in 1979.

Hedycarya arborea (pigeonwood) (Fig. 6)

Pigeonwood flowered from October to December, and developing green fruit was then available until the following January when most of it ripened. Possums usually ate only the flesh of pigeonwood

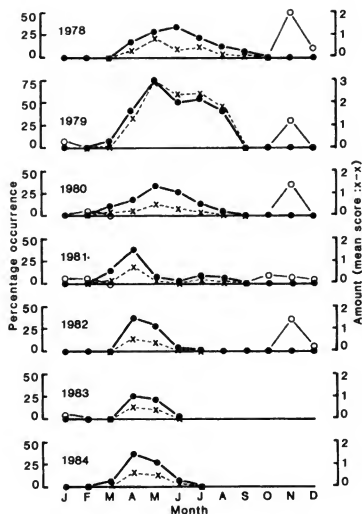


Fig. 5 Percentage occurrence of anthers and stamens from flowers of *Elaeocarpus dentatus* (○), and percentage occurrence (●) and mean score of amount of fruit flesh (x-x) in possum faeces.

fruits, and only ripe fruit, even though green fruits were available for most of the year. Seeds were recorded in only 8 months during the study compared with 31 months for fruit skin. The remains of broken pigeonwood seeds were found mainly in

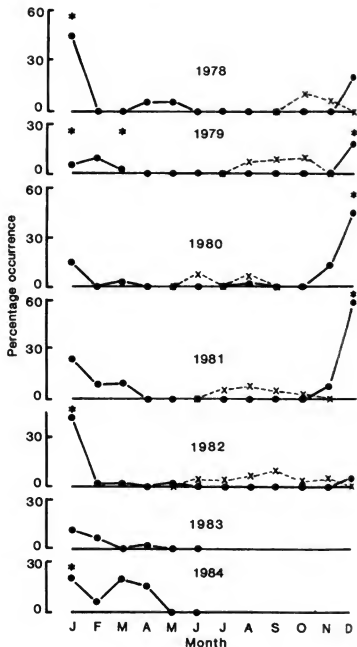


Fig. 6 Percentage occurrence of flesh of *Hedycarya arborea* in possum faeces (●), percentage occurrence of broken seedcases (x), months in which whole seeds were found (*).

Table 4 Dates of first and last ripe fruit fall, total number of fruit falling, and estimated date by which 50% of fruit had fallen under karaka trees (* estimated totals based on single counts in late March).

Tree	Date of first ripe fruit		Date of last ripe fruit		Estimated date of 50% fall		Total numbers of fruit falling			
	1981	1983	1981	1983	1981	1983	1981	1982*	1983	1984*
Q5	27/1	18/1	4/3	6/4	18/2	2/3	546	<200	60	<100
00704	27/1	27/1	10/3	11/4	20/2	2/3	136	>1000	232	>1000
A8	4/2	2/3	24/2	14/3	10/2	2/3	15	<50	4	<50
B8	27/1	8/2	3/3	6/4	14/2	16/3	1250	<50	1175	<100
D5	27/1	18/1	23/3	16/4	16/2	14/3	1937	<50	821	<200

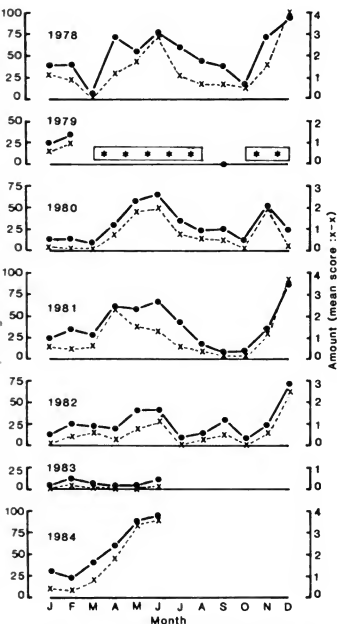


Fig. 7 Percentage occurrence and mean score of amount of flowers and fruits of *Knightia excelsa* in possum faeces. During most of 1979, only presence (*) was recorded.

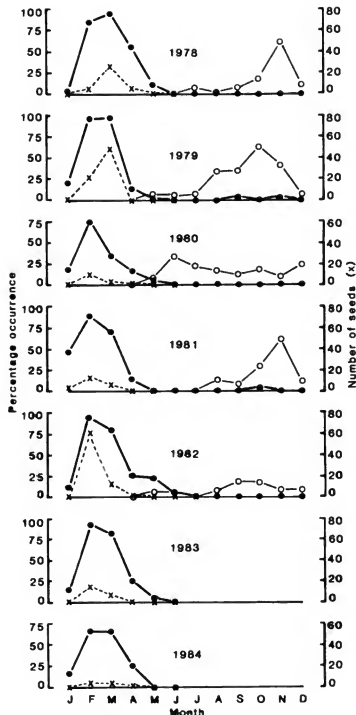


Fig. 8 Percentage occurrence of male flower spikes of *Macropiper excelsum* (O) and percentage occurrence (●) and mean number of seeds (x) in possum faeces.

winter and spring; from their colour and size, they were old seeds from fruit which had ripened earlier the same year, and were probably eaten on the forest floor shortly after germination.

Possums ate pigeonwood fruit from November to March, and occasionally in other months, but mostly in December and January, the same months when most seeds were found in the litter cones. Percentage occurrence in November to February varied significantly among years ($\chi^2 = 59.48$, $P < 0.001$) with occurrence in 1980/81 and 1981/82 significantly greater than in each of the other years (P s < 0.01).

Knightia excelsa (rewarewa) (Fig. 7)

Rewarewa flowered from November to January, with peak flowering in December. Developing flower buds were present, however, from the previous June onwards. Developing fruits were available from January to June, and ripe fruits from March to September. Rewarewa flowers and fruit were eaten by possums throughout the year, but with a sharp peak in November and December and a second more prolonged peak from April to June,

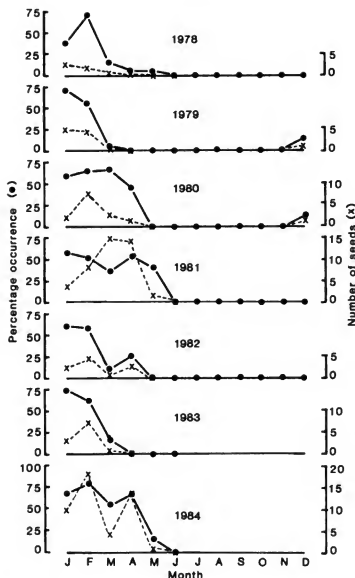


Fig. 9 Percentage occurrence and mean number of seeds of *Melicytus ramiflorus* in possum faeces.

corresponding to the periods when flowers and ripe fruit, respectively were most available. For both flowering (November to January) and fruiting (January to June), the proportions of possums feeding on rewarewa varied significantly between years ($\chi^2 = 23.5, 172.5$, respectively; $P_s < 0.01$). Fewer possums ate rewarewa flowers in 1980/81 and 1982/83, and rewarewa fruits in 1980 and 1982, than in other years ($P_s < 0.05$).

The mean score estimate of amount eaten showed a similar bimodal distribution, with highest scores in April to July and November and December. Overall, the proportion of samples in which rewarewa was common varied significantly between years ($\chi^2 = 30.29, P < 0.01$), with occurrence in 1978 and 1981 significantly greater ($P < 0.05$) than in other years. The relative proportions of samples with few, medium, or common amounts of rewarewa varied significantly during the main fruiting period

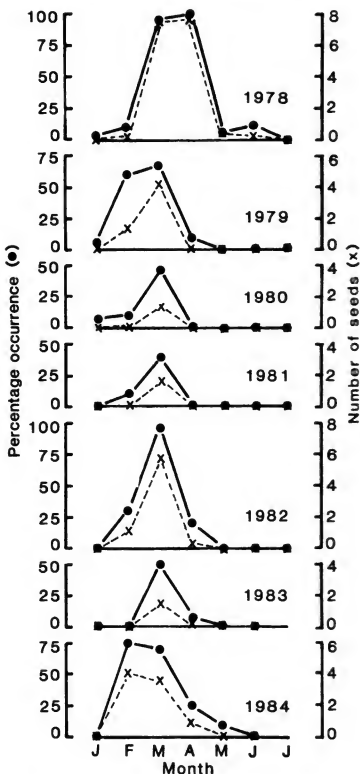


Fig. 10 Percentage occurrence and mean number of seeds of *Pennantia corymbosa* in possum faeces.

($\chi^2 = 42.58, P < 0.01$), but not during the flowering period ($P > 0.3$). Amounts eaten during fruiting in 1982 and 1983 were significantly less than in other years ($P_s < 0.05$).

Macropiper excelsum (kawakawa) (Fig. 8)

Possums ate not only the fruit of kawakawa but also the developing male flower spikes. Male flower spikes

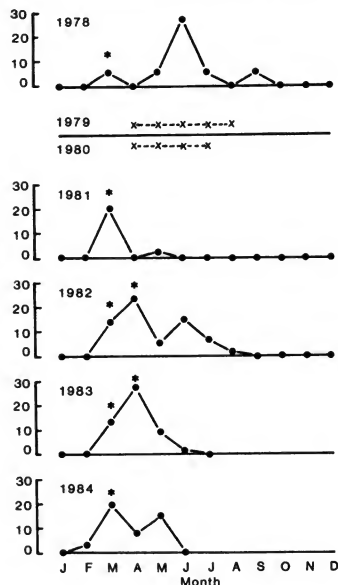


Fig. 11 Percentage occurrence of the flesh of *Rumex crispus* fruit in possum faeces. In 1979 and 1980 only presence (X) was recorded. (*) Months in which seeds were found.

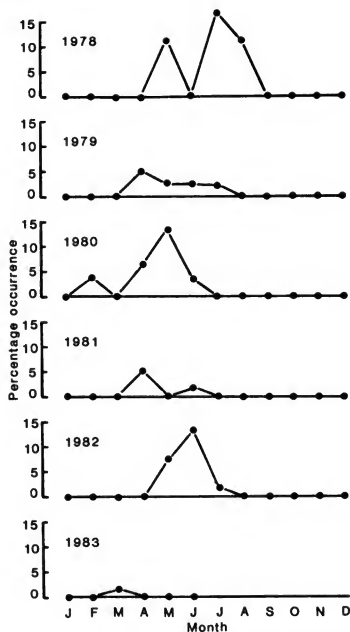


Fig. 12 Percentage occurrence of seeds of *Pseudopanax crassifolius* in possum faeces.

were present from May onwards, growing slowly until they matured in October and November. Male kawakawa flowers were eaten mostly in August to November. Their consumption did not differ significantly between years ($F_{4,24} = 1.17$, $P > 0.2$), but the number of anthers per faecal pellet was greatest in 1978 and 1981. Kawakawa fruit was extensively eaten, particularly in February and March, with no significant variation in percentage occurrence between years ($F_{6,30} = 1.45$, $P > 0.2$). Fewest kawakawa seeds were eaten in 1984 ($P_s < 0.05$), and most in 1979 and 1982 ($P_s < 0.01$). The years when most fruit was eaten (1979 and 1982) followed the years when most male flowers were eaten (1978 and 1981). In 1983 and 1984, 43.5% of 625 seeds in possum droppings were broken.

Melicope ramiflora (mahoe) (Fig. 9)

Mahoe generally flowered from November to February, bore unripe fruit from December to February, and ripe fruit from January to May. Mahoe fruit were eaten by possums each year from December to May, but mostly in January to April. The numbers of possums eating mahoe fruits in December to May varied significantly between years ($F_{6,30} = 4.85$, $P < 0.005$), with fewer eating fruit in 1977/78, 1978/79, 1981/82, and 1982/83 than in other years and most in 1983/84 ($P_s < 0.01$). The numbers of mahoe seeds eaten also varied significantly from year to year ($F_{6,561} = 4.01$, $P < 0.001$). More seeds were eaten in 1980/81 and 1983/84 than in all other years ($P_s < 0.02$).

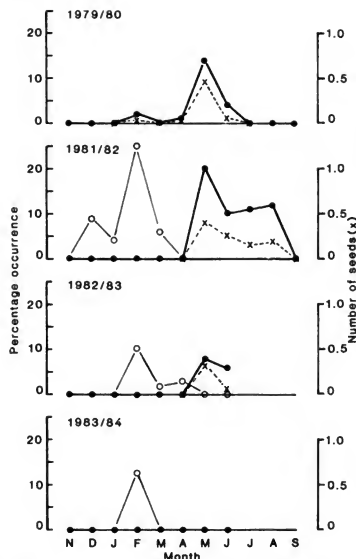


Fig. 13 Percentage occurrence (●) and mean number of seeds (X) of *Passiflora tetrandia*, and percentage occurrence of flowers of *Rhopalostylis sapida* (○) in possum faeces. No *P. tetrandia* seeds were found in 1978, 1979, 1981, or 1984.

Pennantia corymbosa (kaikomako) (Fig. 10)

Kaikomako flowered from late November to January, but primarily in December. Ripe fruit was available from February to April and occasionally to June. Kaikomako fruits were eaten from January to June, but most commonly in February. The numbers of possums eating the fruit varied significantly between years ($F_{6,30} = 2.52$, $P < 0.05$). Percentage occurrence in January to June in 1980, 1981, and 1983 was significantly lower than in other years ($P_s < 0.01$). The mean number of kaikomako seeds per faecal pellet varied significantly between years, with numbers significantly higher in 1978 than in other years ($P_s < 0.05$ at least). Fewest seeds were eaten in 1980, 1981, and 1983 ($P_s < 0.05$) and most in 1979, 1982,

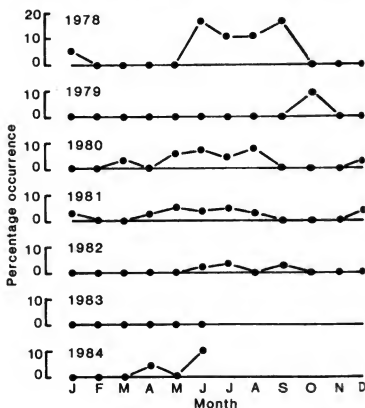


Fig. 14 Percentage occurrence of seeds of *Solanum aviculare* in possum faeces.

and 1984 ($P_s < 0.05$). In 1982 to 1984, 22% of 512 seeds in possum droppings were broken. Passage of kaikomako seeds through a possum's gut did not render all seeds sterile, and 6 out of 13 seeds from faeces of three different possums in April 1984 were successfully germinated.

Prunnopytis taxifolia (matai) (Fig. 11)

Possums usually ate only the flesh of matai fruits. Seeds were only found occasionally, always in March or April; none were found in 1979 or 1980. Matai fruit skin was most commonly found from March to June, with no significant variation in occurrence between years ($\chi^2 = 7.33$, $P > 0.1$).

Pseudopanax crassifolius (lancewood) (Fig. 12)

Lancewood flowered from February to April. A few possums ate lancewood fruit each year, except in 1984. Fruit was eaten in February to August, but mostly in April to July, and often when not fully ripe, as most of the seeds were immature. Occurrence varied among years ($\chi^2 = 8.39$, $P < 0.1$) and was greatest in 1978, 1980, and 1982.

Passiflora tetrandia (kohia) (Fig. 13)

Kohia flowered in November and December. Ripe orange fruit were seen on the vines from April to August, but most often in May to July. Kohia seeds

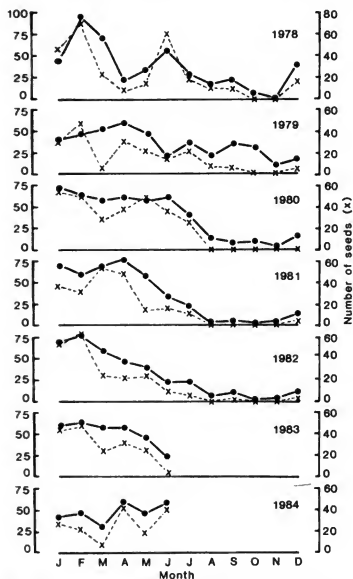


Fig. 15 Percentage occurrence and mean number of seeds of *Urtica ferox* in possum faeces.

ere not found in possum droppings in 1981 or 1984, and only once in each of May 1978, and May and August 1979. They were more commonly eaten in 1980, 1982, and 1983 from May onwards. Occurrence in 1982 was significantly greater than in either 1980 or 1983 ($P_s < 0.05$), and fruits were eaten for a longer period. In 1982, 25% of 57 seeds in possum droppings were broken.

hoplostylis sapida (nikau) (Fig. 13)

Nikau on the study area flowered between December and April, but most commonly in February and March. The anthers of male flowers and the sepals were found in possum droppings each year in at least one month during November to April. Percentage occurrence during 1981–84 was greatest in February, and in 1981/82. No nikau seeds were found in possum droppings during 1978–83, but

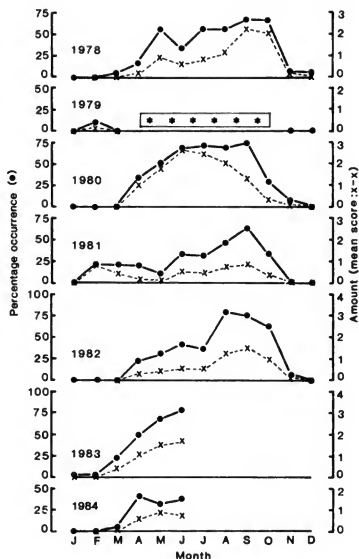


Fig. 16 Percentage occurrence and mean score of amount of buds and flowers of *Ulex europaeus* in possum faeces. For most of 1979, only presence (*) was recorded.

only one of the nine nikau growing on the study area bore ripe fruit during that time.

Solanum aviculare (poroporo) (Fig. 14)

Poroporo flowered and fruited unpredictably. Some poroporo fruit was eaten by possums each year. Seeds were found in droppings in most months, particularly during May to September. Occurrence was greatest in 1978 and least in 1979.

Urtica ferox (onga onga) (Fig. 15)

Onga onga flowered in November and December, and ripe and ripening fruit was available from December to September, but primarily in January to May. After May, much of the remaining fruit had dried out. Onga onga fruit were eaten most commonly from January to July, particularly January to April, though in all years some fruit were eaten

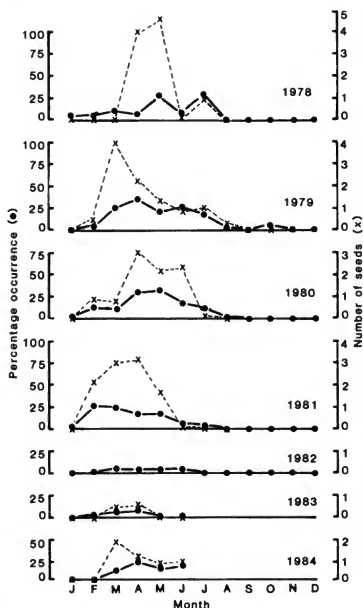


Fig. 17 Percentage occurrence and mean number of seeds of *Solanum nigrum* in possum faeces. Few seeds were found in 1982.

throughout the year. The numbers of possums eating the fruit did not vary significantly between years, either for whole years ($F_{4,44} = 0.83, P > 0.2$) or when only the first 6 months of each year was considered ($F_{6,30} = 1.42, P > 0.1$). Pellets with > 100 seeds were assigned a score of 150. The mean number of seeds eaten was greater in 1978, 1980, and 1982 than in 1979 ($P_s < 0.01$), and greater in 1978 than in 1981 ($P < 0.05$). Similar results were obtained when numbers eaten in the first 6 months of each year were analysed. Pellets with > 100 seeds were more common from January to July, and only rarely occurred after August. In most years, such pellets occurred most often in January and February, with

a second smaller peak of occurrence in May to July.

Other native plants

Fleshy fruits of several other native plants were eaten only occasionally. Seeds of *Coprosma* spp. occurred in only 12 out of 72 months of the study, with 10 out of 12 occurrences in January to May; most were either *C. areolata* or *C. robusta*. Only one supplejack seed (*Ripogonum scandens*) was found in possum droppings, in January 1980, although small amounts of red flesh were found occasionally, and may have been from supplejack or nikau fruits. Seeds of pate (*Schefflera digitata*) were recorded only in June 1978, March 1979, and January 1984. Seeds of totara (*Podocarpus totara*), mapau (*Myrsine australis*), rohutu (*Neomyrtus pedunculata*), and *Nertera depressa* were each recorded in only 1 month during the study.

Seeds of native plants which did not produce fleshy fruits were also found occasionally. Kanuka seeds (*Kunzea ericoides*) were found in January, April, and June 1978, February to April and July 1982, February to June 1983, and January, February and April 1984. Manuka seeds (*Leptospermum scoparium*) occurred only in December 1978, June to August 1982, February and March 1983, and January and April 1984. *Uncinia uncinata*, various Gramineae, *Carex geminata*, and *Gahnia* sp. were also eaten occasionally.

Introduced fruits and flowers eaten by possums

Ulex europaeus (gorse) (Fig. 16)

Gorse flowered throughout the year, but mostly in September and October. Few gorse flowers or flower buds were eaten by possums during November to March. Their occurrence in the diet of possums, and the amount eaten, then increased steadily through the rest of the year to a peak generally in August and September. The overall occurrence of gorse in possum diet varied significantly between years, both for full years ($\chi^2 = 9.04, P < 0.05$), and when occurrence in the first 6 months was considered separately ($\chi^2 = 56.50, P < 0.01$). The mean score index of amount also varied significantly between years ($\chi^2 = 79.48, P < 0.001$). Most gorse was eaten in 1980 ($\chi^2 = 25.38, P < 0.01$). Amounts eaten in the first 6 months also varied significantly between years ($\chi^2 = 20.99, P < 0.01$), with more eaten in 1980 than in all other years except 1983 ($P_s < 0.01$). Gorse seeds were rarely recorded, being found in only 5 out of 72 months of the study.

Nolana nigra (black nightshade) (Fig. 17) lack nightshade flowered mostly in summer and autumn. Fruits of black nightshade were mostly eaten by possums in February to June. Percentage occurrence in January to June varied significantly between years ($F_{5,30} = 6.42$, $P < 0.01$), with occurrence in 1979, 1980, and 1981 significantly greater than in other years ($P_s < 0.05$). Fewest seeds or pellet were found in 1979 ($P_s < 0.05$).

Other introduced plants

Seeds of *Stellaria media* (chickweed) and *Oxycarpus tetraphyllum* (allsed) were recorded in possum faeces each year from October to May. Other introduced plants whose seeds were recorded occasionally included at least six species of iridaceae, two species of plantain (*Plantago* spp.), oxglove (*Digitalis purpurea*), prickly sow thistle (*Sonchus asper*), sow thistle (*Sonchus oleraceus*), and Scotch thistle (*Cirsium vulgare*).

DISCUSSION

The present methods of quantifying the fruits and flowers in the diet of possums were adopted because of recently highlighted problems with commonly used methods based on identifying and measuring plant epidermis (Barker 1986a, b; Norberry 1988). Measurement of relative frequency of occurrence of plant material in faeces may additionally be subject to large errors because of differential digestibilities of leaves, flowers, and fruits (Fitzgerald 1976), and differential rates of passage through the digestive system of different sized remains (Foley & Hume 1987).

Flowers of four native plants (hinau, rewarewa, kawakawa, and nikau) and one introduced plant (gorse) were eaten consistently by possums. Small amounts of unidentified flower remains were also recorded in all months during late spring and summer, so that consumption of flowers was undoubtedly underestimated. Fitzgerald (1976, 1978) recorded possums in the Orongorongo Valley feeding on the flowers of hinau, pigeonwood, rewarewa, and northern and climbing rata. Mason (1958) found flowers of northern rata, five-finger, kamahi, fuchsia, and *Leptospermum* spp. in stomach contents of possums from the same general area, and noted signs of possum feeding on flowers of *Astelia* sp., mahoe, and nikau (plus other species not found on the present study area). Possums have not previously been reported eating male flowers of kawakawa, but they did so mainly in November when the

flowers matured and had developed pollen. Possums feed extensively on the pollen cones of other species, particularly *Pinus radiata* (Clout 1977; Warburton 1978). Gorse flowers are frequently eaten by possums on farmland (Gilmore 1967; Harvie 1973) and in exotic forest (Warburton 1978), particularly in winter and spring.

Possums ate most species of fleshy fruits available on the study area. Fruits of a few species—rewarewa, hinau, karaka, kawakawa, kaikomako, mahoe, and onga onga—were available and were eaten extensively by possums each year. Fruits of putaputaweta, lancewood, poroporo, and pigeonwood were also eaten each year, but in varying amounts. Other species common on the study area but which did not fruit every year, such as kohia, kokaha, matai, and totara, were eaten whenever available. The extensive nature of possum frugivory was also indicated by the wide variety of other fruits eaten occasionally, or by only a few possums; these were mostly of species which were rare on the study area. Coleman et al. (1985) also observed that possums ate a wide variety of fruits, but only a few species in any numbers.

Fruits of some fleshy-fruited species present on the study area were not recorded in the diet of possums. *D. dacrydioides* and *S. microphylla* occurred only as juvenile plants. All *A. excelsus* and *B. tawa* trees were severely defoliated, produced only a few flowers each year, and set no fruit. No *R. cissoides* fruit was seen on the vines. *A. serrata*, *S. fasciculata*, and *M. australis* were all uncommon and fruited sparsely each year. Most of the *Coprosma*s on the study area were small-leaved divaricating species, whose growth habit may discourage browsing (Atkinson & Greenwood 1989). However, fruits of *Coprosma* spp. were commonly eaten in podocarp/mixed hardwood forest in Westland (Coleman et al. 1985). Flesh of *P. ferruginea* fruit has a high resin content and may be unpalatable (Cambie 1976), although the fruits are eaten occasionally (Coleman et al. 1985). Fruits of *G. lucida* were usually eaten by birds before they were ripe.

The numbers and sizes of plants recorded in the vegetation survey gave a general measure of the availability of flowers and fruits, which was not greatly altered by correcting for the sex ratios of dioecious species (Godley 1964). The fruits which featured most often in the diet of possums were mostly those from the most abundant terrestrial and epiphytic plants, except karaka, hinau, and onga onga which were favoured, and *C. areolata* which

was hardly eaten. The distinct seasonality of fruit consumption was also dictated by availability, since most species on the study area bore ripe fruit only in late summer and autumn, and possums did not eat developing fruits. Coleman et al. (1985) similarly observed that fruits eaten by possums generally reflected their availability in the forest.

The high proportions of possums eating flowers and fruits, and the large numbers of fruits eaten, indicated the importance of these items in the diet of possums. This contrasts with their diet in their native Australia. Flowers and fruit are eaten seasonally there, but only in small amounts (Fitzgerald 1984; Kerle 1984), except possibly in tropical rainforest where 28% of food items were flowers or fruit (Proctor-Grey 1984). The lack of fruits in the diet of possums in Australia may, however, simply reflect a lack of woody plant species with fleshy fruits. The closely related *T. arnhemensis* which inhabits the tropical regions of Australia, feeds extensively on flowers and fruits (Kerle 1985). In Tasmania and Victoria, brushtail possums feed on pine pollen cones and are a pest in orchards (Troughton 1967; Statham 1984).

Introduced possums ate large numbers of fruits which would otherwise have been available to native animals. The fruits eaten by possums in the Orongorongo Valley are all also eaten by the native frugivorous birds there—bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*), pigeons (*Hemiphaga novaeseelandiae*), and silvereyes (*Zosterops lateralis*) (P. E. Cowan & M. N. Clout, unpubl. data; Leathwick et al. 1983).

Possums also functioned as seed predators. C. J. West (pers. comm.) found that possums destroyed 69% of the tawa (*Beilschmiedia tawa*) seed in Pureora Forest in 1982. Mason (1958) recorded destruction of seeds of pigeonwood and tutu. In addition, much of the New Zealand flora appears to have seeds adapted for bird dispersal (Clout & Hay 1989) so the 4-fold to 12-fold increase in gut passage time through possums compared with birds may affect subsequent germination (Gilmore 1966; Ziswiler & Farner 1972; Wellard & Hume 1981; Herrera 1984).

However, possums also dispersed seeds. In the Orongorongo Valley, faeces containing seeds were deposited throughout home ranges which average 0.9–1.5 ha (Ward 1978) and in the summer and autumn, possums often make excursions outside their normal ranges to feed on fruiting trees or to breed (Jolly 1976; Ward 1978). Seed dispersal by possums may be of particular importance to native

species with large-seeded fruits, such as pigeonwood, hinau, and matai, as the extinction or marked decline in numbers of New Zealand's large frugivorous birds has left those species with few dispersers (Clout & Hay 1989). Conversely, possum dispersal of seeds may also be exacerbating the spread of introduced weeds (Bass 1990).

In the Orongorongo Valley, the fat reserves of possums increase markedly between December and February (unpublished data), at the time when the largely leaf diet is supplemented with flowers and fruits (Fitzgerald 1976). Although new foliage is also available then (Fitzgerald 1976; Leathwick 1984), and there are seasonal changes in the relative amounts of the various species of leaves eaten (Fitzgerald 1978; Coleman et al. 1985), there are no clear relationships between the changes in the leaf diet and the increased fat deposition (Fitzgerald 1976, 1978; Coleman et al. 1985). Fruits are generally more digestible than leaves, providing a greater intake of energy per unit dry matter (Williams 1982). The partial replacement of leaves by fruit in summer and autumn thus appears to provide a nutritional surplus which is transferred into fat reserves. The size of these fat reserves is affected by the annual variations in availability of fruit, and has consequent effects on reproduction and survival (Bell 1981). The general availability of fleshy fruits may be one more factor which has enabled possums to colonise New Zealand's lowland forests and maintain such high densities compared with their native Australia.

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Use of day-degree estimates for rearing management of *Ctenopseustis obliquana* (Lepidoptera: Tortricidae) in the laboratory

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Abstract The brownheaded leafroller (BHLR), *Ctenopseustis obliquana* (Walker) (Lepidoptera: Tortricidae) was reared on an artificial diet at seven constant temperatures. The mean life cycle at optimum rearing temperature of $20 \pm 1^\circ\text{C}$ was: egg development 8.7 days; larval period, M 37.4, F 11.2 days; pupal period, M 14.9, F 13.3 days; pupal weights, M 50.5, F 68.2 mg; and a fecundity of 670 eggs per female. Estimated lower threshold temperatures and mean cumulative number of day-degrees for various stages of development were 8°C and 105D° for eggs, 5.2°C and 538D° for larvae, and 7.2°C and 186D° for pupa. Total mean day-degree accumulation from egg to adult was 299D° .

These data were used to develop an efficient rearing management system embracing colony maintenance, storage, manipulation, production, and quality assessment procedures.

Keywords *Ctenopseustis obliquana*; brownheaded leafroller; Lepidoptera; Tortricidae; day-degrees; life cycle; temperature; lower threshold temperatures; fecundity; colony maintenance; insect rearing

INTRODUCTION

The brownheaded leafroller (BHLR), *Ctenopseustis obliquana* (Walker) (Lepidoptera: Tortricidae), is a major pest of pip and stone fruits, kiwifruit, berry fruit, and forestry in New Zealand (Green 1979; Kay 1979). A description of the life cycle in the field has been given by Green (1979). Further studies on the bionomics, pest management, and control on apples were done by Green (1984) and Tompkins (1984).

Clare & Singh (1988) carried out a detailed study of life cycle development in the laboratory on an artificial diet at $20 \pm 1^\circ\text{C}$. A colony maintenance system was set up for the supply of experimental insects required for various research programmes (Clare et al. 1987). Because of increased demands for insects and the need for precisely defined life stages defined for experiments, manipulation of the insects' development by use of temperature was needed. Therefore, a study of life cycle development was carried out at a number of constant temperatures on an artificial diet. The lower threshold temperature, rate of development, and cumulative number of day-degrees (D°) were calculated for each stage. These parameters were used in rearing management and the supply of experimental test insects.

MATERIALS AND METHODS

Rearing and colony maintenance

Artificial diet, rearing method, handling, and colony maintenance system are described by Clare & Singh (1988). Life cycle development studies were carried out in controlled temperature rooms maintained at seven constant temperatures of 10, 12, 15, 18, 20, 22, and $25 \pm 1^\circ\text{C}$, with a photoperiod of 18 h and a relative humidity ranging from 50–80%.

Eggs from several batches were collected within 7 h of oviposition and between 200–800 were incubated at each temperature. These were checked daily; upon hatching, the days to first hatch, mean hatch, total hatch, mortality, and fertility were recorded.

Initially, 190–380 neonate larvae were selected at random and reared individually in 75 × 12 mm polystyrene test tubes containing 1.5 g of artificial diet at each temperature. After 2 days all the test-tubes were checked and only those larvae established on the diet were used in life cycle development calculations. When final instars were nearing the pre-pupal stage, larvae were checked daily for pupation. Larval development included the prepupal period. Pupae were extracted, sexed, and weighed within 48 h of pupation. Deformed pupae were not weighed. Pupae were observed daily until adult eclosion and the pupal period and percent survival recorded.

Adults were mated within 8 h of eclosion and total fecundity and fertility for each pair was recorded. A detailed study of daily mean egg laying rates of individual ($n=20$) and group mated adults ($n=45$, 15 pairs/cage) was carried out at $20 \pm 1^\circ\text{C}$.

The Students *t*-test was used to determine significant differences in life cycle parameters by the statistical programme MINITAB (Ryan et al. 1976).

Calculations

1. *Lower threshold temperatures* for any given stage were determined either by: (a) The equation

$$D1(T1-K) = D2(T2-K),$$

where $D1$ = mean duration time at minimum temperature in days

$D2$ = mean duration time at maximum temperature in days

$T1$ = minimum rearing temperature

$T2$ = maximum rearing temperature

K = the lower threshold temperature in $^\circ\text{C}$, an unknown constant. The equation is then calculated for K .

(b) Plotting a straight line regression of the rate of development (expressed as the reciprocal of days to development) against temperature, and extrapolation through the x axis provides an estimate of the lower threshold temperatures (Arnold 1959).

or (c) A similar graph as in (b) can be plotted with rate of development expressed as D° per day [rearing temperature (T) minus lower threshold (K)]. This confirmed the value for K obtained in (a).

2. *Development rate per day in day-degrees* for each life cycle stage and temperature was calculated by subtracting the rearing temperature (T) from the estimated lower threshold temperature (K), expressed as $T-K = D^\circ/\text{day}$.

3. *The cumulative number of day-degrees* for each life cycle stage at each temperature (T) were calculated by multiplying development rate per day

($T-K$) in D° by mean duration time of development in days (D). This is expressed as $(T-K) \times D$.

RESULTS AND DISCUSSION

Egg development. The mean time required for development of eggs varied from 46.1 days at 10°C to 6.4 days at 25°C (Table 1 and Fig. 1). The duration of hatch (days from first to total hatch) also varied from 4 days at 10°C to 0.6 days at 25°C . Mortality ranged from 3–14% except at 25°C where it was 33%. Development rate (expressed as day-degrees per day) between 10°C and 25°C varied more or less linearly with temperature (Fig. 1A). A straight line fitted by regression, of rate of development per day against temperature, intersected the temperature axis at 7.8°C . This is an estimate of the lower threshold temperature for eggs. Regression equation of rate of development per day is given by the formula $y = -7.8 + 1.0x$, where x = temperature. The mean cumulative number of D° required for development was $105D^\circ$.

Larval period. Mean larval developmental periods are shown in Table 2 and Fig. 1B. Survival ranged from 85–98% at the seven temperatures. The regression equation for rate of development per day versus temperature, for males and females combined, was $y = -5.2 + 1.0x$. The estimated lower threshold temperature is 5.2°C (Fig. 1B). The mean cumulative number of D° required for larval development was 529 and $547D^\circ$ for males and females, respectively, with a combined mean of $538D^\circ$.

Pupal weight. There were significant differences ($P < 0.001$) between male and female pupal weights at the seven temperatures (Table 3). Mean pupal weights ranged from 49–60 mg and 63–71 mg for males and females, respectively. There were no

Table 1 Duration (days), percent mortality and day-degree accumulations (D°) of the egg stage of *C. obliquana*

Temp. No. of					
($^\circ\text{C}$)	eggs	Mean \pm SE	range	% Mortality	Total D°
10	702	46.1 ± 0.05	43.5–47.5	9.8	101
12	741	24.3 ± 0.01	24.0–25.0	4.8	102
15	468	13.4 ± 0.02	12.9–13.9	3.0	97
18	594	10.2 ± 0.03	9.5–11.0	13.8	104
20	784	8.7 ± 0.07	8.0–8.8	10.0	106
22	826	7.9 ± 0.09	7.3–8.0	3.5	112
25	209	6.4 ± 0.02	6.0–6.6	32.7	110
Mean				105	

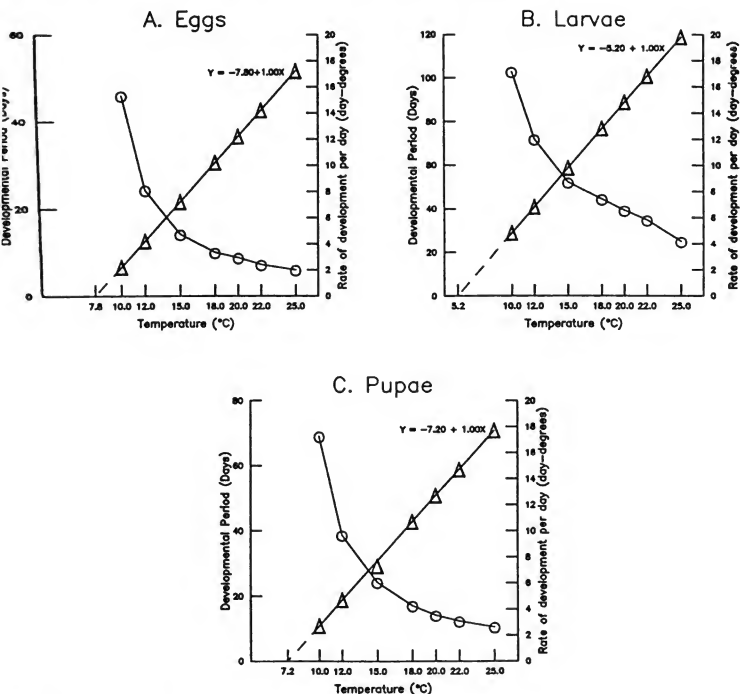


Fig. 1 Period (○) and rate of development (△) of *C. obliquana* eggs, larvae, and pupae in relation to temperature.

significant differences between the temperatures, except at 25°C, where the pupal weights were 39 mg for males and 50 mg for females, respectively, weights which were significantly lower for both sexes ($P < 0.001$).

Pupal period. Male pupal periods were significantly longer than those of females at all temperatures ($10^\circ\text{C} = P < 0.05$; $12\text{--}25^\circ\text{C} = P < 0.001$) (Table 4). Survival ranged from highs of 91% at 18°C and 95% at 20°C, to lows of 65% at 25°C and 78% at 10°C. The mean estimated lower threshold temperature for male and female pupal development

combined, obtained by regression, was 7.2°C ; the regression equation of development rate versus temperature was $y = -7.2 + 1.0x$ (Fig. 1C). The mean cumulative number of D° for pupal development was 195 and 177 D° for males and females, respectively, with a combined mean of 186 D° .

Adult fecundity. The highest mean fecundity of 670 was obtained at 20°C ($P < 0.001$) with over 80% fertility (Table 5). No eggs were laid at 22 and 25°C, indicating that higher temperatures inhibited egg laying in adults. No fecundity data were recorded at 12°C.

A comparison of daily mean egg laying rates derived from individually paired adults ($n=20$) and group-mated adults (15 pairs/cage, 3 replicates) at 20°C is shown in Fig. 2. Adults of both groups reached peak egg laying on days 2–4 after pairing; >50% of eggs were laid by day 4 and 80% by day 6 in both instances. Individually mated adults laid a mean of 144 more eggs ($P<0.001$) than group mated females.

Rearing management of *C. obliquana*

Insect rearing management (IRM) has been defined as the efficient utilisation of resources for the production of insects of standardised quality to meet programme goals (Singh & Ashby 1985). In the development of an IRM system for any species, the gathering of life cycle development data at a number of constant temperatures, using a standardised diet and rearing technique, is absolutely essential. From a practical rearing management point of view, it is advantageous to express rate of development as D° per day (T–K), for each stage of development as represented in Fig. 1. In the development of IRM for *C. obliquana*, life cycle parameters and day-degree estimates for each stage were applied as follows:

1. Optimum colony maintenance temperature. The optimum temperature range for insect rearing is that where the insects maintained in the laboratory will develop and reproduce at a desired (usually

maximum) rate and are of required quality (Ashby & Singh 1987). The development times, pupal weights, percent survival, fecundity, and fertility are extremely useful indicators for choosing the optimum temperature for development of all stages. From the life cycle data (Tables 1–5 and Fig. 1, 2), 20 ± 1°C was chosen as the optimum temperature for larval rearing, pupation, and oviposition for *C. obliquana*. This temperature gave the quickest development period with the highest percent survival, fecundity, and 80% fertility. Above 20°C no eggs were laid.

2. Colony maintenance system. Colony maintenance has been defined as the level of biological productivity needed to continuously maintain a laboratory colony at a sustained required level (Ashby & Singh 1987). Generally, colonies required for insect production are maintained at a stable level. The schedule remains static, with no change in the number of insects produced. This system is desirable when there is a steady demand for all the insects produced. However, if there are times when few or no insects are required, it is wasteful in time, labour, money, and resources to maintain production at the same stable level.

In the IRM approach, insect colonies are kept at a minimum maintenance level and their size is regulated depending on demand. The schedules are planned in advance and can be regulated. Rearing and handling procedures are standardised. The advantages of this type of system is that it is flexible, reliable, efficient, and there is minimum wastage of insects and resources.

Table 2 Larval development (days), day-degree accumulations (D°) and percent survival for *C. obliquana*.

Temp. (°C)	Sample Size	Sex	n	Mean ± SE	Min	Max	Total D°	% survival (M & F)
10	184	M	85	101.3 ± 0.7	91	117	486	85
		F	72	104.5 ± 0.8	94	120	502	
12	185	M	95	71.1 ± 0.7	59	90	484	98
		F	86	72.7 ± 0.7	64	90	495	
15	180	M	91	51.7 ± 0.3	47	58	507	92
		F	74	52.7 ± 0.3	47	61	517	
18	308	M	143	45.2 ± 0.4	37	56	579	89
		F	132	44.8 ± 0.3	35	53	573	
20	363	M	175	37.4 ± 0.2	31	47	554	91
		F	154	41.2 ± 0.2	35	47	610	
22	150	M	67	36.3 ± 0.9	30	57	610	87
		F	64	37.0 ± 0.6	30	56	622	
25	157	M	77	24.3 ± 0.3	20	30	481	89
		F	63	25.8 ± 0.3	22	31	511	
Mean D°		M				529		547
		F						
		M & F						538

Table 3 Pupal weights (mg) of *C. obliquana*.

Temp. (°C)	Sex	n	Mean ± SE	Min	Max
10	M	85	50.4 ± 0.6	39.7	62.3
	F	72	63.4 ± 0.9	40.0	83.6
12	M	79	54.7 ± 1.0	41.2	80.4
	F	65	70.5 ± 1.1	52.9	86.3
15	M	89	60.4 ± 0.8	47.7	77.7
	F	67	70.7 ± 1.1	51.0	100.2
18	M	141	56.7 ± 0.7	42.1	101.6
	F	126	68.9 ± 0.9	42.8	98.3
20	M	174	50.5 ± 0.5	33.7	63.8
	F	154	68.2 ± 0.7	47.7	106.0
22	M	66	49.0 ± 1.2	22.3	73.1
	F	64	66.6 ± 2.0	18.8	100.9
25	M	77	38.6 ± 0.7	17.7	63.8
	F	63	50.2 ± 0.8	35.0	62.7

For determining the appropriate size of the maintenance colony and for calculating insect supplies, a detailed study of oviposition, showing daily mean egg laying rates for individual and group mated adults at 20°C was done (Fig. 2). This enabled the prediction of the number of eggs available per lay per female from a given colony size.

The life cycle parameters, percentage yields, and standardised rearing procedures at the optimum temperature of 20 ± 1°C, enabled a minimum, stable level of production to be determined. Fig. 3 modified from Clare et al. (1987) shows the IRM system of colony maintenance for *C. obliquana*. This consisted of inoculation of four larval-rearing containers per week producing a total of 280 pupae. Eighty pupae were selected for eclosion (40 ♂ and 40 ♀) with the remainder going to storage. Thirty pairs of adults were divided into two group-oviposition cages (15 pairs/cage) which yielded a total of 15 000 eggs. With 80% fertility, the yield was 12 000 fertile eggs. One-thousand of these eggs were placed at 20°C of which 800 were used for inoculation of four new larval-rearing containers. The remainder went to storage (see below).

3. Insect storage system. Insect storage is the maintenance, at a low temperature or in diapause, of insects that are the result of overproduction or that are to be used later (Ashby & Singh 1987).

Table 4 Pupal period (days), day-degree accumulations (D°) and percent survival for *C. obliquana*.

Temp. (°C)	Sample Size	Sex	n	Mean ± SE	Min	Max	Total D°	% survival (M & F)
10	157	M	66	70.7 ± 1.2	49	93	198	
		F	57	67.3 ± 1.0	51	84	188	78
12	181	M	75	41.0 ± 0.3	36	46	197	
		F	74	36.3 ± 0.3	31	43	174	82
15	165	M	77	25.9 ± 0.2	21	29	202	
		F	62	22.8 ± 0.1	20	26	178	84
18	275	M	131	18.3 ± 0.1	17	21	198	
		F	119	15.9 ± 0.1	14	19	172	91
20	329	M	166	14.9 ± 0.1	13	17	191	
		F	146	13.3 ± 0.1	12	15	170	95
22	131	M	54	12.6 ± 0.1	11	14	187	
		F	50	11.9 ± 0.1	11	13	176	79
25	140	M	52	10.9 ± 0.1	9	12	194	
		F	39	10.1 ± 0.1	8	13	180	65
Mean D°		M				195		
		F				177		
		M & F				186		

That is, the "shelf life" of insect stages can be extended by keeping them at a lower than normal temperature for as long a period as possible without significant changes in their quality. In any colony maintenance system, excess insects are always produced. These are valuable as a potential backup colony, as spare insects for supply, or for increasing the size of the colony.

The egg and pupal stages of *C. obliquana* were stored at 10°C (Fig. 3). Excess eggs, (14 000 collected over a period of 2 weeks from two cages) were stored for use for up to 6 weeks before being discarded. Two-hundred excess pupae were sexed and stored for up to 9 weeks until adult emergence. Adults emerging from pupae were used or held at 10°C for up to 2 weeks before being discarded. Development of such a storage system is invaluable as it provides a potential source of various stages of development at all times.

4. Insect manipulation. Manipulation is the use of temperature, photoperiod, or some other environmental variable to adjust the development rate of a population in the laboratory (Ashby & Singh 1987). Day-degree estimates obtained by calculation from the life cycle data at different temperatures can be used in the manipulation of insects. Day-degrees have been defined as units of measurement which relate temperature and time to stages of insect development (Ashby & Singh 1987). Hardman (1976) states that a given species of insect has different thresholds of development for each developmental stage. Therefore, D° are directly related to the lower threshold temperature of particular stages. The lower threshold temperatures and mean cumulative number of day-degrees for various stages of development for *C. obliquana* were 7.8°C and 105D° for the egg, 5.2°C and 538D° for the larva, and 7.2°C and 186D° for the pupa; the total day-degree accumulation from egg to adult was 829 day-degrees.

Table 5 Fecundity and fertility of *C. obliquana*.

Temp. (°C)	n	Mean ± SE	Min	Max	% Fertile
10	34	252 ± 16	146	397	98
12		No data recorded			
15	21	95 ± 19	0	318	62
18	22	132 ± 20	0	327	73
20	20	670 ± 60	0	1021	81
22	20	No eggs laid			
25	26	No eggs laid			

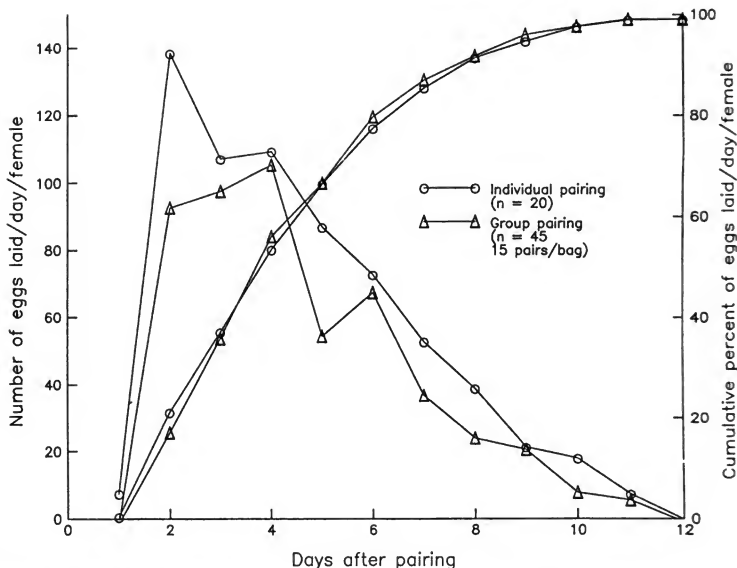


Fig. 2 Daily mean egg-laying rates and daily cumulative percent egg-laying of *C. obliquana* at $20 \pm 1^\circ\text{C}$.

Manipulation of a particular stage can be achieved by varying the temperature and making use of the life cycle and D° data. Fig. 1 can be used as a quick and easy guide to obtaining this information. Summary tables can also be prepared for each stage and/or sex showing mean, minimum, and maximum D° per day, and total D° accumulation at each temperature. These are time savers when planning insect supplies. Tables can also be prepared giving D° per day from day 1 up to the mean D° accumulation at each temperature for each stage by the formula $(T-K) = D^\circ/\text{day}$ as shown in Table 6. This table can be used as a ready reference when manipulating larvae of different ages to synchronise their development. For example, Table 6 shows for *C. obliquana* that development in 1 day at $20 \pm 1^\circ\text{C}$ is equal to $14.8D^\circ$ which is about equal to 3 days development at $10 \pm 1^\circ\text{C}$ ($14.4D^\circ$). This information ensures the synchronisation and manipulation of

insects to meet required supply dates. Also, the work can be spread over a number of days thus maximising staff effectiveness. Co-ordinating supplies of lepidopterous larvae by manipulating their development time with temperature has been reported by Ng et al. (1987). Manipulation of the life cycle stages by temperature and "day-degrees" and their subsequent use in "storage" is a key to IRM.

5. Insect production. This is defined as the rate of productivity of a laboratory insect population as measured by the number or weight of eggs, larvae, nymphs, pupae, or adults that can be produced per unit time (Ashby & Singh 1987). To produce a known number, stage, and age of insects, as well as supplying them on a specific date, requires developmental data and life cycle manipulations. Fig. 4 shows the percentage of each stage of development per day from neonate larva to adult

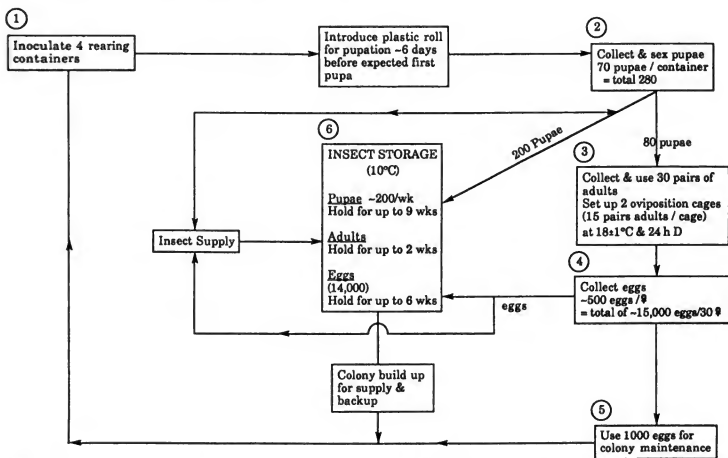


Fig. 3 Steps in colony maintenance system for *C. obliquana* at $20 \pm 1^\circ\text{C}$ and 18h L:6 hD (Modified from Clare et al. 1987).

Table 6 Day-degree estimates per day for *C. obliquana* larval development at constant temperatures. (Mean lower threshold temperature = 5.2°C Mean total day-degree accumulation = 538 D°)

Days	10	12	15	18	20	22	25
1	4.8	6.8	9.8	12.8	14.8	16.8	19.8
2	9.6	13.6	19.6	25.6	29.6	33.6	39.6
3	14.4	20.4	29.4	38.4	44.4	50.4	59.4
4	19.2	27.2	39.2	51.2	59.2	67.2	79.2
5	24.0	34.0	49.0	64.0	74.0	84.0	99.0
27.2	538
32.0	538	.
36.4	538	.	.
42.0	.	.	.	538	.	.	.
54.9	.	.	538
79.1	.	538
112.1	538

for *C. obliquana*. Two development times, the 50% and 90%, are highlighted to allow quick reference for all stages to the specific day of development on which these occur. For example, Fig. 4 shows that 90% of 4th instar larvae occur on day 19 at $20 \pm 1^\circ\text{C}$. Similarly, the first pupa and adult will occur on day 30 and 46, respectively. This information is indispensable when planning the production and supply of various stages for a specified date. The principles discussed here were applied in the codling moth production system (Singh & Clare in press).

6. Quality assessment. This is an integrative procedure that develops, maintains, and improves quality; it is a regulatory process through which quality of performance is measured and compared with standards, and which acts on any difference (Ashby & Singh 1987). Quality standards for each stage of development are set over time by comparing each generation with the mean of the previous generations. Life cycle data and D° are an aid in producing large numbers of high quality insects of known age, stage, and performance. These enable quality standards for all stages to be established which can then be monitored per generation or

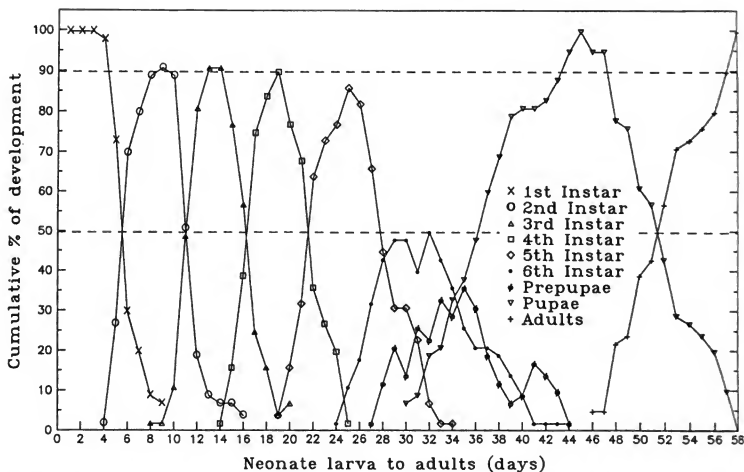


Fig. 4 Development of *Ctenopseustis obliquana* from neonate larva to adult on artificial diet at $20 \pm 1^\circ\text{C}$, 18h L:6hD and 50–60% RH.

when supplying insects. For example, pupal weight, adult fecundity, and fertility of *C. obliquana* are three parameters which are monitored each generation. Pupal weights falling within 10 mg either side of the means (41–61 mg for males and 58–78 mg for females) were considered of acceptable quality at 20°C . Adult fecundity at 20°C was monitored and indicated a mean of 670 eggs with 80% fertility which was used as a quality standard.

Since these studies were completed Clare & Singh (1988) have found that at $20 \pm 1^\circ\text{C}$, *C. obliquana* has two distinct 5 and 6 larval instar groups. We have further found (Clare & Singh 1990) that there are differences in life cycle parameters between the two groups and these can affect quality assessment standards. Quality assessment is therefore an extremely important aspect of any rearing system where insects of defined quality are required for on-going research.

In conclusion, this study on *C. obliquana* has shown the importance of obtaining life cycle data, lower threshold temperatures, and day-degree estimates for life stages. The advantages of using

these parameters in the development of an IRM system are:

1. The optimum temperature for colony maintenance can be determined.
2. The colony maintenance system can be regulated.
3. An insect storage system can be established.
4. Insects can be manipulated and produced with precision on specified dates.
5. Insects of defined quality can be produced.
6. A reduction of peak demand on "rearing staff" time and resources can be achieved.

We recommend that these concepts be practised in multiple insect rearing laboratories responsible for the production and supply of quality experimental insects on which depends the success of many entomological programmes.

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Morphological characterisation of the entomogenous nematodes *Steinernema* spp. and *Heterorhabditis* spp. (Nematoda: Rhabditida)

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Abstract Infective juveniles and adults of 8 steinernematid and heterorhabditid strains were characterised using 11 standard morphometric characters. Differentiation between strains was attempted for individuals by comparing the range of measurements for each character; populations were differentiated by comparing the means for each character. I concluded that morphometric methods still have use for designation of steinernematid strains to the specific level. However, DNA characterisation methods now available should be adopted for intraspecific steinernematid differentiation, and specific and intraspecific heterorhabditid differentiation.

Keywords *Steinernema*; *Heterorhabditis*; morphometrics; DNA fingerprinting

INTRODUCTION

Entomogenous nematodes of the genera *Steinernema* and *Heterorhabditis* (Nematoda: Rhabditida) form specific symbiotic associations with bacteria of the genus *Xenorhabdus*

(Eubacteriales: Enterobacteriaceae). The infective stage of the nematodes actively seek and penetrate insects, voiding *Xenorhabdus* cells into the haemocoel where a septicemia develops, killing the insect and supporting nematode growth and reproduction (Poinar & Thomas 1966).

Species of *Steinernema* and *Heterorhabditis* vary in their ability to migrate and infect insect hosts (Bedding et al. 1983; Wright et al. 1989); this variation extends to the intraspecific level (Molyneux 1983; Wright & Jackson 1988). Because of this behavioural and physiological variation it is important to characterise and distinguish between closely related species and strains of *Steinernema* and *Heterorhabditis*.

Until recently, nematodes were almost solely characterised by morphology and associated morphometric observations. Commonly, larval and adult morphometric characters have been incorporated into de Man indices or ratios (Southey 1978). Poinar (1986) found infective larvae total length and ratio E (distance from head to excretory pore divided by length of tail) useful characters to distinguish between species of *Steinernema*, but considered other ratios too variable to be of use. Differentiation between strains of the same species of *Steinernema* has been difficult. Poinar (1986) showed that four strains of *S. feltiae* (= *Neoaeplectana carpocapsae*) overlap in range of all five larval characters the strains were compared with.

The development of macromolecular analyses, particularly of nucleic acids and proteins, have eased greatly characterisation of a wide variety of prokaryotes and eukaryotes. Curran et al. (1985) and Curran & Webster (1987) have already shown that electrophoretic analysis of restriction endonuclease DNA fragments can facilitate specific designation of *Steinernema* and *Heterorhabditis* strains.

Because of these new techniques, a study was undertaken to determine the future use of traditional morphometric characterisation methods for differentiating between species and strains of *Steinernema* and *Heterorhabditis*.

MATERIALS AND METHODS

Nematode strains used in this study are listed in Table 1.

Table 1 Source of nematode strains examined.

Strain	Source
Steinernematids	
CA	Canterbury, N.Z. <i>Agrotis ipsilon</i> larva
AKLD	Auckland, N.Z. <i>Graphognathus leucomela</i> larva
OHIO	Ohio, USA <i>Popillia japonica</i> larva
<i>S. glaseri</i>	Ohio, USA <i>Popillia japonica</i> larva
Heterorhabditids	
HNZ	Auckland, N.Z. <i>Heteronychus arator</i> adult
HL81	Holland
V16	South Australia <i>Graphognathus leucomela</i> larva
HNA	Ohio, USA <i>Popillia japonica</i>

Nematodes were propagated in last instar *Galleria mellonella* L. larvae (Lepidoptera: Galleriinae) at 20°C. First generation steinernematid adults and first generation heterorhabditid females were dissected from 3-day old cadavers and heterorhabditid males from 7-day old cadavers. Infectives were induced to emerge from cadavers after 2 weeks incubation using a water trap. All nematodes were heat killed (80°C), fixed in TAF, and processed to glycerin as described by Poinar (1975).

For each strain, 30 infective and 30 male nematodes were measured, and 10 female nematodes examined using differential interference contrast on a Carl Zeiss microscope (Oberkochen, West Germany). Measurements were made through Zeiss Plan 16 (×160) and Plan 40 (×400) objectives and recorded as units of an eyepiece scale.

Table 2 Mean, standard deviation (SD), and range of measurements for 10 characters of steinernematid infectives (all measurements in µm).

Character		Strain			
		<i>S. glaseri</i>	CA	OHIO	AKLD
Total length	Mean	1306	781	540	866
	SD	143	59	33	58
	Range	1019–1507	680–1010	475–610	734–1001
Greatest Width	Mean	65	34	27	27
	SD	10	5	2	3
	Range	47–90	27–43	24–32	23–32
Dist. Head–Excret. Pore	Mean	ND	53	33	60
	SD		3	4	3
	Range		50–59	25–41	54–65
Dist. Head–Pharynx Base	Mean	149	112	111	138
	SD	12	11	7	9
	Range	126–178	90–149	99–126	122–153
Length Tail	Mean	101	54	44	85
	SD	13	5	6	5
	Range	79–119	43–61	34–50	74–92
Ratio A	Mean	20	23	20	33
	SD	2.9	2.8	1.5	3.8
	Range	13–26	18–27	17–33	27–43
Ratio B	Mean	8.8	7.0	4.9	6.3
	SD	0.8	0.5	0.2	0.4
	Range	7.1–10.5	5.5–8.1	4.6–5.2	5.4–7.1
Ratio C	Mean	13.1	14.6	12.6	10.2
	SD	1.3	1.4	1.9	0.5
	Range	10.3–15.5	12.6–17.6	10.5–16.7	9.3–11.2
Ratio D	Mean	ND	0.48	0.30	0.44
	SD		0.04	0.04	0.03
	Range		0.38–0.6	0.2–0.39	0.39–0.48
Ratio E	Mean	ND	0.99	0.78	0.71
	SD		0.09	0.17	0.04
	Range	1.15–1.34	0.85–1.16	0.52–1.2	0.63–0.81

Note. ND = Not determined.

Table 3 *F*-Value, LSD, and strain groupings for measurements of 10 steinernematid infective characters.

Character	<i>F</i> -value	LSD	Strain groupings ³			
			<i>S. glaseri</i>	CA	OHIO	AKLD
Total Length	296.61*	44.6 ²	a	b	c	d
Great. Width	285.0*	2.7	a	b	c	c
Head Ex.pore	287.9*	1.9	ND	b	c	d
Head-PharynxB	84.6*	5.2	a	b	b	c
Tail Length	329.5*	3.7	a	b	c	d
Ratio A	111.5*	1.45	a	b	a	c
Ratio B	211.0*	0.27	a	b	c	d
Ratio C	81.9*	0.65	a	b	c	d
Ratio D	113.3*	0.020	ND	a	b	c
Ratio E	71.9*	0.060	ND	a	b	c

¹*F*-Values with an asterisk (*) are significant ($P=0.05$)²Fisher's least significant difference values ($P=0.05$)³Strains not having the same letter for a particular character are significantly different ($P=0.05$) at the population level.

ND = not determined

Table 4 Mean, standard deviation (SD), and range of measurements for 11 characters of steinernematid males (all measurements in μm).

Character		Strain			
		<i>S. glaseri</i>	CA	OHIO	AKLD
Total length	Mean	1342	971	777	921
	SD	72	93	85	62
	Range	1172–1499	752–1116	619–934	767–1001
Greatest width	Mean	61	60	54	77
	SD	8	6	7	12
	Range	50–77	50–77	36–68	59–95
Dist. head–Excret. pore	Mean	ND	81	47	76
	SD		4	5	8
	Range		74–90	32–54	59–92
Dist. head–Pharynx base	Mean	159	130	113	130
	SD	10	7	10	13
	Range	142–173	117–146	97–130	104–162
Length tail	Mean	26	29	20	28
	SD	3	3	4	2
	Range	20–32	25–36	16–30	23–34
Ratio A	Mean	22	17	15	12
	SD	3.0	2.4	2.0	2.1
	Range	18–29	12–20	11–19	8–17
Ratio B	Mean	8.5	7.5	6.9	7.2
	SD	0.63	0.71	0.78	0.93
	Range	7.1–9.6	6–9	5.5–9.4	5.7–9.5
Ratio C	Mean	52	33	40	33
	SD	6.2	3.8	6.9	3.1
	Range	38–67	24–41	23–52	28–41
Ratio D	Mean	ND	0.63	0.42	0.59
	SD		0.056	0.05	0.07
	Range		0.54–0.74	0.3–0.54	0.46–0.74
Ratio E	Mean	ND	2.8	2.4	2.8
	SD		0.31	0.47	0.32
	Range		2.4–3.6	1.1–3	1.2–3.6
Spicules	Mean	64	58	47	62
	SD	5	2	4	2
	Range	52–74	54–61	38–56	56–65

ND = not determined

Measurements recorded were of distances between, and lengths of, structures indicated by the descriptions given by Poinar (1979), Wouts (1980), and Poinar et al. (1987). The following ratios were calculated using the formulae given by Poinar (1986): A (total length divided by width), B (total length divided by distance from head to base of pharynx), C (total length divided by length of tail), D (distance from head to excretory pore, divided by distance from head to base of pharynx), and E (distance from head to excretory pore divided by length of tail).

Eyepiece to micron conversions, statistical descriptions, and ratios were calculated using MINITAB on a VAX 11/780 computer. Statistical comparisons between strains for each character involved a two-step process. Analysis of variance (ANOVA) (Little & Hills 1978) was conducted with the whole group of steinernematid or

heterorhabditid strains. If a significant F -value ($P = 0.05$) was recorded for a particular character, Fisher's least significant difference test (Fisher 1966) was used to determine which strain(s) differed significantly from other strains for that character. The Student's t test ($P = 0.05$) (Little & Hills 1978) was performed to compare male characters of strains CA and AKLD.

Strain comparisons were described for individuals by comparing ranges of the characters for each strain; and for populations by statistical inferences concerning the mean differences between strain measurements.

RESULTS

Based on the descriptions given by Chitwood & Chitwood (1937), the strains *S. glaseri*, AKLD, CA,

Table 5 Mean, standard deviation (SD), and range of measurements for 10 characters of heterorhabditid infectives (all measurements in μm).

		Strain			
Character		HNA	HL81	V16	HNZ
Total length	Mean	773	708	602	547
	SD	71	43	50	40
	Range	617-880	585-779	511-691	450-630
Greatest Width	Mean	32	25	23	22
	SD	4	4	4	1
	Range	25-38	20-32	19-32	20-26
Dist. Head-Excret. Pore	Mean	123	115	113	96
	SD	6	6	8	7
	Range	108-131	101-124	99-133	83-108
Dist. Head-Pharynx Base	Mean	156	140	134	115
	SD	8	10	10	8
	Range	140-171	128-149	117-149	97-126
Length Tail	Mean	87	75	60	58
	SD	6	5	3	3
	Range	79-101	68-86	52-65	52-63
Ratio A	Mean	24.7	28.5	26.3	24.8
	SD	2.5	3.9	2.8	1.8
	Range	18.3-29.8	18.6-37.2	21.5-31	20.9-28
Ratio B	Mean	5.0	5.1	4.5	4.8
	SD	0.28	0.22	0.45	0.22
	Range	4.4-5.5	4.5-5.6	3.9-5.9	4.3-5.3
Ratio C	Mean	9.0	9.5	10.1	9.4
	SD	1.1	0.64	0.63	0.61
	Range	6.9-10.9	8.2-10.7	9.1-11.4	8.4-10.4
Ratio D	Mean	0.79	0.82	0.85	0.84
	SD	0.03	0.03	0.05	0.03
	Range	0.72-0.86	0.76-0.87	0.77-0.93	0.78-0.91
Ratio E	Mean	1.42	1.54	1.90	1.65
	SD	0.11	0.11	0.13	0.12
	Range	1.11-1.56	1.29-1.73	1.64-2.22	1.39-1.88

Table 6 *F*-Value, LSD, and strain groupings for measurements of 10 heterorhabditid infective characters.

Character	<i>F</i> -Value	Strain groupings ³				
		LSD	HNA	HL81	V16	HNZ
Total length	115* ¹	24.10 ²	a	b	c	d
Great. width	51.7*	1.59	a	b	c	c
Head-ex.pore	77.9*	3.04	a	b	b	c
Head-pharynxB	124*	3.78	a	b	c	d
Tail length	262*	2.07	a	b	c	c
Ratio A	12.6*	1.33	a	b	c	a
Ratio B	18.5*	0.14	a	a	b	c
Ratio C	10.04	0.36	a	b	c	b
Ratio D	33.9*	0.018	a	b,c	c,d	d,b,c
Ratio E	85.2*	0.057	a	b	c	d

¹All *F*-Values with an asterisk (*) are significant ($P=0.05$) except ratio C.²Fisher's least significant difference values ($P=0.05$)³Strains not having the same letter for a particular character are significantly different ($P=0.05$) at the population level.**Table 7** Mean, standard deviation (SD), and range of measurements for 11 characters of heterorhabditid males (all measurements in μm).

Character		Strain			
		HNA	HL81	V16	HNZ
Total length	Mean	943	979	927	870
	SD	100	84	84	95
	Range	743–1102	848–1190	767–1082	747–1112
Greatest width	Mean	47	51	42	63
	SD	3	5	3	6
	Range	41–54	43–61	36–50	47–70
Dist. head–Excret. pore	Mean	160	138	139	152
	SD	14	5	8.5	
	Range	133–185	128–146	121–153	135–162
Dist. head–Pharynx base	Mean	126	114	117	113
	SD	4	4	9	4
	Range	117–135	106–122	99–135	104–122
Length tail	Mean	38	38	34	34
	SD	4	2	5	2
	Range	29–45	34–41	25–43	29–38
Ratio A	Mean	20.4	19.4	21.9	13.9
	SD	2.9	2.0	1.7	2.1
	Range	15.0–26.6	16.4–23.0	19.1–25.6	11.5–19.4
Ratio B	Mean	7.5	8.6	7.9	7.7
	SD	0.7	0.78	0.43	0.84
	Range	6.4–8.8	7.3–10.2	7.3–8.8	6.5–9.5
Ratio C	Mean	25.1	25.7	27.6	25.7
	SD	2.4	1.9	3.8	2.5
	Range	19.8–29.7	21.3–29.8	22.6–38.5	21.0–30.9
Ratio D	Mean	1.27	1.22	1.19	1.35
	SD	0.12	0.04	0.07	0.06
	Range	1.05–1.46	1.14–1.32	0.98–1.34	1.20–1.47
Ratio E	Mean	4.26	3.64	4.15	4.49
	SD	0.45	0.25	0.57	0.28
	Range	3.5–5.0	3.22–4.13	3.11–5.64	3.94–5.31
Spicules	Mean	47.6	51.4	47.0	50.0
	SD	3.4	1.7	1.9	3.7
	Range	41–59	50–56	43–50	45–59

and OHIO were confirmed as belonging to the Steinernematidae. The strains HNA, HL81, V16, and HNZ fitted the description of family Heterorhabditidae given by Poinar (1975). Heterorhabditid infectives could be distinguished readily from steinernematid infectives, steinernematids having the excretory pore anterior to the nerve ring, heterorhabditids having it posterior. Male steinernematids lacked a caudal bursa supported by papillae, structures found with all heterorhabditid males examined.

The range, mean, and standard deviation for each character measured are presented in Tables 2 (steinernematid infectives), 4 (steinernematid males), 5 (heterorhabditid infectives), and 7 (heterorhabditid males). The *F*-value, LSD, and strain groupings for the same characters are presented in Tables 3 (steinernematid infectives), 6 (heterorhabditid infectives), and 8 (heterorhabditid males).

Steinernema spp. infectives

S. glaseri. Compared to the species description given by Poinar (1986), the strain of *S. glaseri* measured here corresponded well in both total length and ratio E, but had a wider range in distance from head to pharynx base. From only 2 of 50 infectives examined, could distance from head to excretory pore be measured with any certainty. Both were within the range given by Poinar (1986). All infectives measured could be distinguished from any other strain of this study, having greater total length and width. At a population level, *S. glaseri*

differed significantly from the other strains ($P = 0.05$) in all measured characters except ratio A.

AKLD and CA. Average measurements of infectives of these strains fell within the range for total length and distance to excretory pore described by Poinar (1986) as criteria for *S. bibionis*. For individuals, AKLD infectives could be separated at an individual level from CA infectives by the tail length and the ratios A, C, and E.

Similarly, AKLD infectives did not overlap with OHIO infectives in distance from anterior to excretory pore, total length, tail length, and ratios A, B, and D.

OHIO. Infectives of this strain corresponded well to the description of *S. feltiae* by Poinar (1986), although the upper limit of ratio E was extended by OHIO infectives to 1.2. All infectives examined differed from infectives of the other steinernematid strains in having shorter distances from head to excretory pore and total length, and smaller ratio B values. At the population level, OHIO was significantly different from the mean of the other strains in 7 of the 10 characters measured and proved identical to CA, AKLD, and *S. glaseri* strains in the distance from the head to pharynx base, width, and ratio A, respectively.

Steinernematid males

Steinernema glaseri males examined lacked a tail spine, had moderately curved spicules, and were longer than any male of the strains CA, AKLD, and OHIO. The distance from head to pharynx base of any *S. glaseri* male was longer than that of any

Table 8 *F*-Value, LSD, and strain groupings for measurements of 11 heterorhabditid male characters.

Character	<i>F</i> -Value ¹	LSD	Strain groupings ³			
			HNA	HL81	V16	HNZ
Total length	1.41	49.32				
Great. width	596* ²	1.16	a	b	c	d
Head-exc.pore	154*	2.67	a	b	c	b
Head-pharynxB	43.3*	2.67	a	b	b	c
Tail length	5.9*	1.87	a	a	b	b
Ratio A	50.7*	1.27	a	a	b	c
Ratio B	5.7*	0.38	a	b	c	a,c
Ratio C	6.9	1.35	a	a	a	b
Ratio D	160.9*	0.02	a	b	c	d
Ratio E	66.3*	0.16	a	b	c	d
Spicules	3.6	1.60				

¹All *F*-Values are significant ($P=0.05$) except for total length, ratio C, and spicules

²Fisher's least significant difference values ($P=0.05$)

³Strains not having the same letter for a particular character are significantly different ($P=0.05$) at the population level.

OHIO male. Males of CA and AKLD were characterised by a long tail spine (6.8–13.5 µm long), indistinct capitulum, and a prominent pair of ventral pre-anal papilla. The range of measurements for distance to excretory pore and ratio D of CA, and distance to excretory pore and length of spicules of AKLD, did not overlap the corresponding ranges recorded for OHIO. The measurements of CA overlapped with those of AKLD for all characters. Significant mean differences, however, were recorded for 7 of the 11 characters: total length, greatest width, distance to excretory pore, tail length, spicules, and ratios A and D. OHIO males possessed a short tail spine (1–3 µm in length), well developed capitulum, and pointed spicules. Ventral pre-anal papillae were not observed. Males of all four strains matched the description of the species indicated previously by the infectives and summarised in Table 9.

Heterorhabditid infectives

None of the strains could be differentiated from all other strains at the individual level by one single character. All strains overlapped in range of total length and ratios A, B, C, and D.

HNA. The measurements recorded here correspond to those given by Poinar et al. (1987) for this strain. The tail lengths of all HNA infectives measured were longer than the tail lengths of all other strains except HL81. Infectives of HNA and HL81 overlapped in the range of measurements for all characters. At the population level, HNA infectives were significantly different to all other strains for all characters except ratios A and B.

HL81. The range of measurements recorded for any character of HL81 infectives overlapped with the corresponding range of all other strains except HNZ in distance from head to pharynx base, and HNZ and V16 in tail length. The mean values for

HL81 infectives were significantly different from all other strain means in distance from head to pharynx base, total length, width, tail length, and ratio E.

V16. Infectives of V16 more resembled the description of *H. bacteriophora* given by Poinar (1975) than of any other published heterorhabditid description. The range of measurements recorded for any character of V16 infectives overlapped with the corresponding range of all other strains except HNA and HL81 in tail length, and HNA in ratio E. At the population level, V16 infectives were significantly different from the other strains only in distance from head to pharynx base and ratio E.

HNZ. The ranges of HNZ infectives did not overlap with those of HNA infectives in distance from head to excretory pore, distance to pharynx base, and tail length. Similarly, HNZ infectives did not overlap with HL81 infectives in the range of measurements for distance from head to pharynx base and tail length. The ranges of HNZ infectives overlapped with those of V16 infectives measured for all characters. Of the heterorhabditid species described, HNZ most resembled *H. bacteriophora* (Poinar 1975).

As a population, HNZ infectives differed significantly from all other strains in the distance from head to excretory pore, distance to pharynx base, total length, and ratio E.

Heterorhabditid males

For all characters examined, the range of measurements for males of any one strain overlapped with those of the other three strains. The heterorhabditid strains could not therefore be separated by examining individual male specimens.

At the population level, there was no significant difference in total length and spicule length between the four strains. HNA males were, however, significantly different from males of the other strains in distance from head to excretory pore, distance to pharynx base, width, and in ratios D and E. HL81 males differed significantly from other strains in width and ratios B, D, and E. The distance from head to pharynx base, width, and ratios A, C, D, and E were all characters of male HNZ nematodes which differed significantly in values to those of the three other strains. Males of strain V16 were significantly different from those of the other strains in distance from head to excretory pore, width, and ratios A, D, and E.

Table 9 Species designation of nematode strains.

Strain	Species
<i>S. glaseri</i>	<i>Steinernema glaseri</i>
CA	<i>S. bibionis</i>
AKLD	<i>S. bibionis</i>
OHIO	<i>S. feltiae</i>
HNA	<i>Heterorhabditis megidis</i>
V16	<i>H. bacteriophora</i>
HL81	<i>Heterorhabditis</i> sp.
HNZ	<i>H. zealandica</i>

Females

Considerable differences were found between the 10 females of each strain examined. Because of the considerable variation within each strain, statistical analyses were not performed and differentiation between strains by comparing females measurements was not attempted.

DISCUSSION

The results here supports previous workers (Stanuszek 1971; Wouts et al. 1982; Poinar 1986) that species of *Steinernema* can be distinguished on the basis of length of individual infectives. Other characters useful for distinguishing between species' infectives, at the population level, were distance from head to excretory pore, tail length, and ratios C, D, and E. In addition, the male spicule morphology differences studied elsewhere (Turco et al. 1971; Bedding pers. comm.), and male tail spine morphology observed here, are useful for species categorisation of steinernematids.

Although strains CA and AKLD both fitted the description of *S. bibionis*, the differences between individual infectives of the two strains in tail length and ratio A demonstrated that subspecific variation among steinernematids exists and can be detected using morphometric analyses. Less obvious were the differences between males of the two strains detected at the population level for 7 of 11 characters.

That none of the heterorhabditid strains could be differentiated from all other strains at the individual level for any one infective character, confirms previous investigations that heterorhabditids are considerably more homogenous than steinernematids (Akhurst 1987). Despite such homogeneity, the results support the description by Poinar et al. (1987) of strain HNA as a distinct species, *H. megidis*. Infectives and males of this strain had significantly different mean values from the other strains for nine and five characters, respectively.

The close resemblance of V16 to *H. bacteriophora* (Poinar 1975) confirmed the electrophoretic patterns of Akhurst (1987) and Curran (pers. comm.) who found V16 most closely related to the type strain of *H. bacteriophora*.

Strain HNZ was found not to resemble any previously described species of *Heterorhabditis*, and as suggested by the electrophoresis study reported by Akhurst (1987) and scanning electron microscopy study by Molyneux (1983), this strain is now considered a new species, *H. zealandica* (Poinar 1990).

As strain HL81 was significantly different from all other strains in infective and male mean values in five and four characters, respectively, and did not fit the description of *H. megidis*, *H. bacteriophora*, or *H. heliothidis*, this strain also probably represents a separate undescribed species.

The homogeneity exhibited by heterorhabditids and the susceptibility of both groups to environmental influences, using morphological and morphometric analyses (Alikhan et al. 1985), illustrates the necessity for more sensitive and definitive methods of characterisation.

Although species determinations have been confirmed by interbreeding studies in the genus *Steinernema*, (Akhurst & Bedding 1978; Poinar 1979), such methods can not be used for differentiating between strains of a *Steinernema* species nor for the self-fertilising heterorhabditids.

DNA electrophoresis has already been shown by Curran et al. (1987) and Curran & Webster (1989) to be able to differentiate between closely related heterorhabditid and steinernematid strains. Such DNA characterisation has corresponded well to the starch/enzyme electrophoresis conducted by Akhurst (1987).

The considerable morphometric variability recorded by this study among steinernematid and heterorhabditid males, and particularly first generation females, has been observed by many other workers (Poinar 1975; Khan et al. 1976; Poinar 1978; Wouts 1979; Poinar et al. 1987). Morphometric analyses of first generation females is considered to have little diagnostic value.

In conclusion, it is suggested that under strict rearing and fixing methods, morphology and morphometric analyses are satisfactory for designation of steinernematid strains to the species *S. glaseri*, *S. bibionis*, and *S. feltiae*. Presently, heterorhabditid strains can only be tentatively assigned to the specific level. Use of single to low copy DNA electrophoretic fragments and specific hybridising probes should be adopted more widely for differentiation between closely related steinernematid and all heterorhabditid strains.

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Further ultrastructural observations on the alveolar epithelium of the newborn rat

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Abstract Typical osmiophilic lamellated bodies of the type II alveolar pneumonocyte of the neonate rat contain parallel, straight lamellae. They often enclose membrane-bounded regions of cytoplasm resembling the sequestered areas in autolysosomes. In other lamellated bodies, the lamellae are less electron dense and are arranged in concentric circles. The concentrically ordered lamellae are eliminated into the alveolar cavity. The osmiophilic lamellated bodies are interpreted as advanced lysosomes.

Mitochondria of the type II alveolar cell are often indented by lamellar masses. Mitochondria enclosing lamellae or dense masses persist for a time after the type I alveolar cell morphology has been attained. Lamellar masses in mitochondria are believed to be related to lysosomal activity in the surrounding cytoplasm, and examples of such inclusions in mitochondria of other tissues are cited. An alveolar cell mitochondrion indented by lamellated material may continue to operate, the mitochondrion proper and the pocket of lysosome-derived lamellae combining as a functional unit.

Keywords alveolar pneumonocyte; ultrastructure; lamellated bodies; glycogenolysis; cytodifferentiation; autophagy; lysosomes; lysosomal enzymes; mitochondria

INTRODUCTION

There are two theories concerning the nature of lamellated bodies in the type II alveolar

pneumonocyte. The bodies have been interpreted as lysosomes by Balis & Conen (1964), Hataza & Nakamura (1965), Sorokin (1966), Corrin & Clark (1968), Goldfischer et al. (1968), Hoffman (1972), DiAugustine (1974), and Williams (1981). According to the alternative view, they represent secretory bodies containing a complex mixture of substances including a surface-active agent which functions to reduce surface tension in the alveoli (references in Campiche et al. 1963; Leeson & Leeson 1964; Caulet et al. 1968; King 1974; Avery 1975; Mason & Williams 1977; Shimura et al. 1985). It has been suggested that the two concepts may be reconcilable if surplus secretory bodies are catabolised by the cellular machinery involved in autophagy of unwanted materials (Hoffman 1972); however, as a general rule, almost all lamellated bodies of the type II alveolar cell show evidence of lysosomal enzyme activities (Balis & Conen 1964; Goldfischer et al. 1968; Kuhn 1968).

The present investigation further explores the basic nature of the osmiophilic lamellated bodies, and the relationship between lamellar material and mitochondria.

MATERIALS AND METHODS

Lobes of lungs excised from newborn rats 2 days post-partum were prepared for electron microscopy according to the schedule detailed previously (Williams 1981). Sections were cut on an LKB Ultratome with diamond knives. They were stained with uranyl nitrate for 30 min, then with lead citrate for 5 min, and viewed and photographed using a JEM-1200 EX electron microscope.

OBSERVATIONS

Type II cell

The type II alveolar cell is characterised by the intensive production of osmiophilic lamellae. The lamellae are found in autolysosomes (Williams 1981); they are also present in the typical

osmiophilic lamellated bodies (OLBs) (Fig. 1, 7), which are composed of parallel, straight lamellae enclosed in a single boundary membrane (Fig. 1; me). Lamellae of an OLB have a trilaminate structure, as is characteristic of membranes (Fig. 7; arrow). The surrounding cytoplasm is rich in glycogen (Fig. 1; gl).

OLBs frequently show membrane-limited, pyriform indentations filled with a relatively electron-clear cytoplasm (Fig. 2, 3; ★), containing dense granules appreciably smaller than glycogen granules found in the general cytoplasm. Cytoplasmic regions of this kind may be completely enclosed within OLBs (Fig. 2; ★); they resemble the sequestered areas contained in autolysosomes (Fig. 2; al).

Occasionally, the lamellae of an OLB appear to be folded into a whorl (Fig. 1; OL) with a quantity of moderately dense, amorphous material at the centre (Fig. 1; am).

Other images of lamellated bodies seen in sections show lamellae organised in concentric circles or a "fingerprint" pattern. The lamellae are faintly demarcated with a reduced osmiophilia, and dense matter is concentrated at the periphery. These bodies are often observed near the free border of the epithelium, and their concentrically arranged contents are found in the alveolar cavity (Fig. 3).

There are two types of multivesicular body in the type II cell, both containing a number of ovoid vesicles: some have a clear matrix within the limiting membrane (see Williams 1981, fig. 3, 4); in others a dense material occupies the intervesicular space (Fig. 4; mvb).

Association with mitochondria

Lamellated bodies composed of stacks of straight lamellae are sometimes found in close association with mitochondria. Fig. 4 shows an OLB continuous with a mass of lamellated material protruding into a mitochondrion. The lamellae of the invaginated portion form a whorl, surrounded by the mitochondrion except for a small area where they are contiguous with the lamellae of the OLB.

Rod-like bodies of high electron density are found in the type II alveolar pneumocyte (Fig. 4; rb). They appear homogeneous except in certain regions where closely packed, longitudinal lamellae with a trilaminate substructure are discernible (Fig. 4; arrow). The rod-like structure in Fig. 4 is invaginated at one end by a mitochondrion.

Lamellated bodies of the concentric type also occur in close relationship with mitochondria. The images of associated concentrically-lamellated

bodies and mitochondria suggest the organelles may be fused or linked in some way (Fig. 5). Sometimes, two mitochondria are discovered associated in this manner with the same "fingerprint" body.

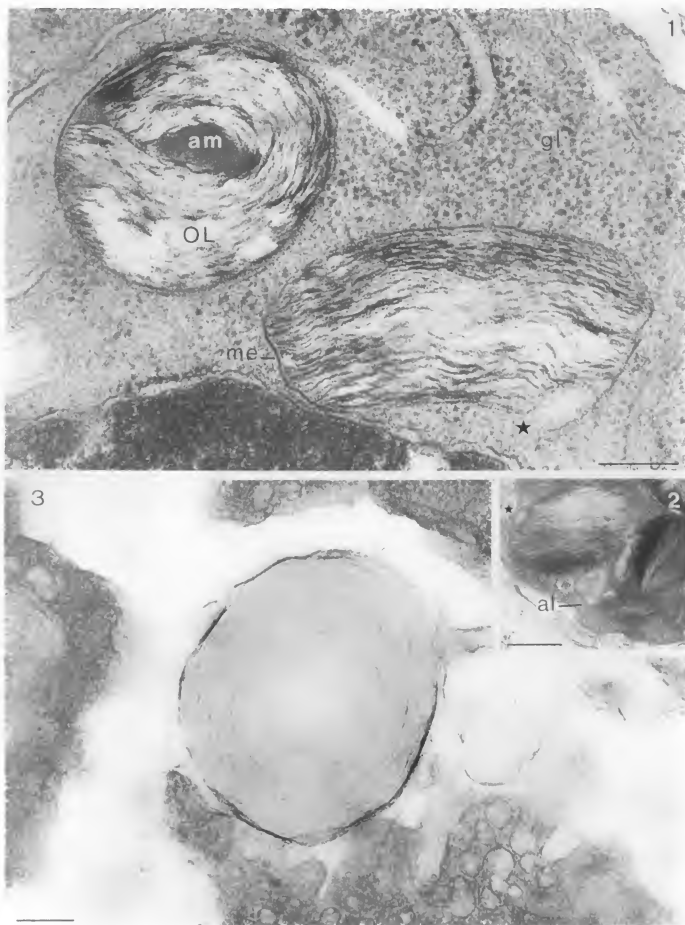
Many lamellar configurations are found to be invaginated by mitochondria (Fig. 6, 7). In places, the lamellae are seen to have the trilaminar composition typical of membranes (Fig. 6; arrow). Also, masses of amorphous material are enclosed by the mitochondria (Fig. 7, am). The inner mitochondrial membrane of the indentations is atypical; it is thinner and less electron dense than the inner membrane of other regions of the mitochondria, and is free of cristae. Long, narrow GER cisternae with a floccular content are spatially associated with the indented mitochondria (Fig. 6, 7; GER). Wide areas of the cisternal membranes are devoid of ribosomes.

Type I cell morphology

Mitochondria are still present after the greatly attenuated type I cytoarchitecture (the mature cell form) has been attained. The mitochondria may contain lamellar configurations (Fig. 8; M), or irregular masses of high electron density in which few lamellae can be seen (Fig. 9; M). Adjacent to many of the indented mitochondria lie Golgi systems (Fig. 8; G), from which arise vesicles similar to those fusing with the surface plasmalemma (Fig. 8; ve). Plentiful glycogen granules remain (Fig. 9; gl).

DISCUSSION

Substances identified in lung foams analysed by Klaus et al. (1961) show a close correspondence with the products of membrane analysis, and analysis of the phospholipid fraction yields typical membrane phospholipids (King 1974; Mason & Williams 1977; Mason et al. 1977). Phosphatidylcholine is the predominant phospholipid constituent, as in all membranes. On the basis of these data and their trilaminate structure, the osmiophilic lamellae of lamellar bodies are interpreted as membrane. Williams (1981) believed that they should be interpreted as the emptied isolation (sequestration) membranes of cellular autophagy, rather than as a complex secretory substance synthesised for the purpose of releasing surface tension-reducing phospholipids at the cell surface. The OLBs are therefore considered to be advanced lysosomes. It is worthy of mention that membrane is a boundary layer, specifically fitted to



g. 1-3. (1) Alveolar type II cell. Osmiophilic lamellated bodies. Scale line 0.25 μ m. (2) Alveolar type II cell. Osmiophilic lamellated body and autolysosome. Scale line 0.5 μ m. (3) Concentric lamellae in alveolar cavity. Scale line 0.25 μ m. al, autolysosome; am, amorphous material; gl, glycogen; me, membrane bounding osmiophilic lamellated body; OL, osmiophilic lamellae. Asterisks, sequestered areas of cytoplasm, enclosed by osmiophilic lamellated body in Fig. 2.

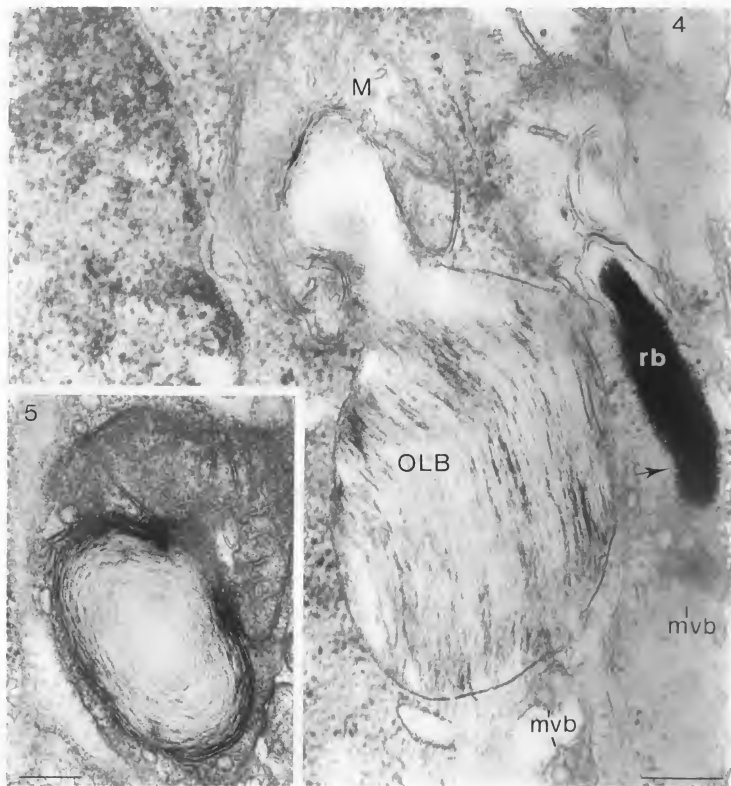
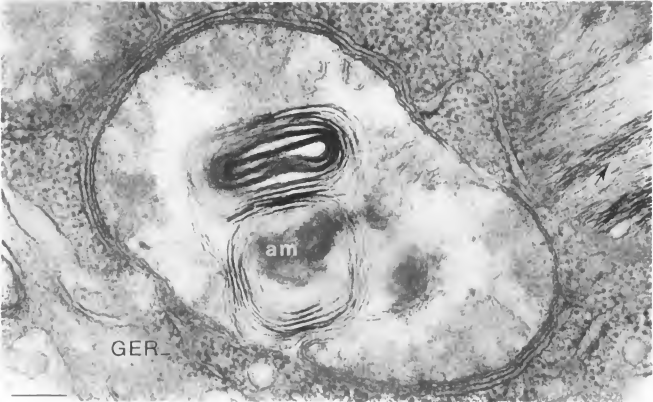
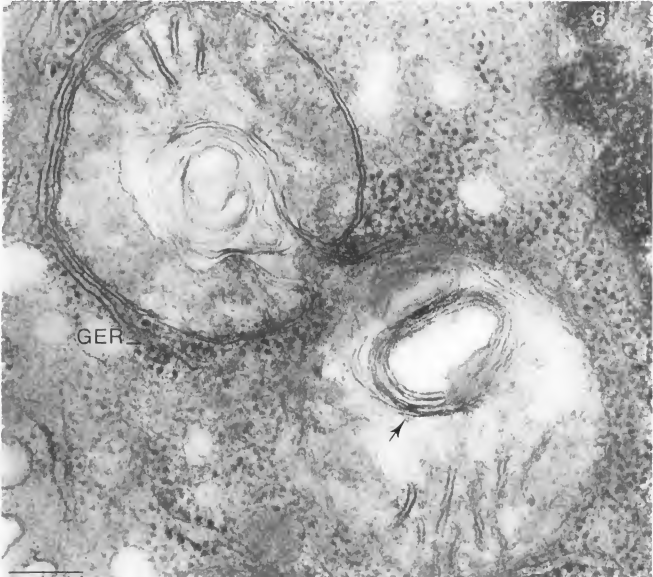


Fig. 4, 5. (4) Alveolar type II cell. Osmiophilic lamellated body associated with mitochondrion. Scale line 0.25 μ m. (5) Concentrically lamellated body associated with mitochondrion. Scale line 0.25 μ m. M, mitochondrion indented by whorl of lamellae; mvb, multivesicular bodies; OLB, osmiophilic lamellated body; rb, rod-like structure invaginated at one end by mitochondrion. Arrow, trilaminar lamellae.

Fig. 6, 7. (6) Alveolar type II cell. Mitochondria indented by lamellae. Scale line 0.25 μ m. (7) Alveolar type II cell. Indented mitochondrion and osmiophilic lamellated body. Scale line 0.25 μ m. am, amorphous material; GER, granular endoplasmic reticulum. Arrow Fig. 6, trilaminar lamellae in mitochondrion. Arrow Fig. 7, trilaminar lamellae of osmiophilic lamellated body.



delimit cells and organelles and to compartmentalise cytoplasm; it is not a secretion in the sense of a substance synthesised by a cell to subserve a function external to the cell.

The OLBs are probably formed from autolysosomes (a type of multivesicular body), and in the normal sequence of events the lamellae are destined for expulsion into the alveolar cavity as concentric accumulations. Evidently a rapid and intensive autophagy occurs in the type II alveolar cell, which in the neonate rat appears to be related to the accelerated tissue differentiation which occurs during the perinatal period.

Glycogen storage and metabolism are clearly important activities of the type II alveolar pneumocyte. The micrographs of Campiche *et al.* (1963) of the human foetal lung show glycogen-rich regions in the developing alveolar epithelium, containing smooth membrane-bounded bodies. Concentrated glycogen deposits surround the bodies, but the membrane-enclosed regions are glycogen free. The authors believed that glycogen granules isolated within these structures had undergone demolition by glycogenolysis. It was suggested by Williams (1981) that the OLBs of alveolar type II cells build up as a result of repeated episodes of glycogenolysis.

The observation of sequestered, granular cytoplasm enclosed within OLBs suggests cytoplasmic regions, possibly containing glycogen, are added to lysosomes at an advanced stage. The process, which may be continuous, probably entails the incorporation of further areas of membrane. Similarly, new areas of segregated cytoplasm destined for lysis are added to advanced lysosomes in the epidermis of starved temnocephalids (Williams 1979).

It is proposed that, once the contents of segregated areas in alveolar cell lysosomes are catabolised, the sequestration membranes themselves undergo degradation by lysosomal hydrolases. Activity of acid phosphatase, the characteristic "marker" enzyme of lysosomes, has been localised in the osmiophilic lamellae (Balis & Conen 1964; Hatasa & Nakamura 1965; Sorokin 1966; Kuhn 1968). Corrin & Clark (1968) and Goldfischer *et al.* (1968) demonstrated additionally the presence of aryl sulphatase activity. DiAugustine (1974) identified specific activities of many typical lysosomal enzymes in purified lamellated material, including acid phosphatase, aryl sulphatase, β -N-acetylglucosaminidase, alkaline phosphatase, glucose-6-phosphatase, β -glucuronidase, α -

mannosidase, β -D-galactosidase, and p-nitrophenylacetate esterase. Meban (1972) demonstrated phosphatidic acid phosphatase activity in the lamellated bodies; this is of particular interest as it provides evidence that the catabolic activity of the bodies can extend to membrane phospholipid substrates.

Membrane accumulations build up when autophagy is rapid and intensive (as typifies the alveolar type II cell), because the sequestration membranes undergo demolition more slowly than their contents. The rate of membrane accumulation in the form of type II cell OLBs may be further accelerated by experimental or clinical procedures, such as glucocorticoid administration (e.g., Ballard 1977) or thyroid hormone administration (Avery 1975). These act to hasten differentiation. Significant membrane accumulations also occur when completion of degradation is blocked because one of the essential lysosomal enzymes is reduced or absent. Specific lysosomal enzymes may be lacking, as in human lipidoses such as Niemann-Pick's disease and Tay-Sachs disease, or experimentally inhibited. In human lipidoses, affected tissues of children genetically incapable of synthesising one of the essential lysosomal hydrolases develop lamellated bodies (Wallace *et al.* 1966; Adachi & Volk 1971), which in some instances are morphologically indistinguishable from alveolar cell OLBs (Adachi & Volk 1971, fig. 3). Acid phosphatase activity is localised in the bodies, and by this criterion they are identified as lysosomes without dissent in the literature.

Masses of membranous lamellae in close association with or enclosed by mitochondria are believed to originate in areas of lysosomal activity in the surrounding cytoplasm (see Williams 1983, 1984). Experimental administration of chloroquine to chickens inhibits certain lysosomal enzymes and enhances autophagy, resulting in an increased number of autophagic vacuoles in the skeletal muscles (Trout *et al.* 1981). These authors found evidence of direct fusion between dense acid phosphatase positive lysosomal structures and mitochondria (Trout *et al.* 1981, fig. 13).

A number of lysosomal enzymes respond to phenobarbital treatment by significantly decreased specific activities. Orrenius & Ericsson (1966) studied liver tissue of phenobarbital-treated rats; some mitochondria of hepatic parenchymal cells were found to be enlarged, enclosing variable amounts of membrane (Orrenius & Ericsson 1966, fig. 11). In some instances the mitochondria



Fig. 8, 9. (8) Type I cell morphology. Indented mitochondrion and Golgi system. Scale line 0.25 μ m. (9) Type I cell morphology. Mitochondrion invaginating dense mass. Scale line 0.5 μ m. G, Golgi system; gl, glycogen; M, indented mitochondria; ve, vesicle at surface resembling Golgi-associated vesicles.

contained considerable membrane accumulations, displaying a close morphological similarity to mitochondria observed in this study.

During temnocephalid spermatogenesis, cytoplasmic reduction is a major contributing factor in the extensive reorganisation of cellular constituents; autophagic processes are augmented in the diminishing cytoplasmic masses during the spermatid stage, and membrane accumulations invaginated by mitochondria are found (Williams 1983, 1984).

Caulet et al. (1968, fig. 10, 12) depicted rat alveolar cell mitochondria with enclosed lamellate masses, resembling mitochondria illustrated in this study. Myelin figures within rat alveolar pneumonocyte mitochondria were observed by Goldenberg et al. (1969) following pilocarpine administration, an experimental procedure which may stimulate all exocytotic processes or accelerate differentiation (Avery 1975). Flaks & Flaks (1972) discovered myelin-like accumulations in mitochondria in cultured explants of a murine pulmonary tumor. The surrounding cytoplasm contained glycogen rosettes.

The micrographs of Sacktor & Shimada (1972) show mitochondria in the flight muscle of aging blowflies. Membrane accumulations (which may be seen in the surrounding cytoplasm in some of the authors' figures) and glycogen granules, similar to those in the glycogen-laden cytoplasm, are enclosed by the mitochondria. These images of mitochondrial inclusions are probably related to glycogenolysis. Similar inclusions may occur in human skeletal muscle mitochondria (Sher et al. 1967, fig. 14).

Lysosomes therefore tend to be associated with mitochondria in a variety of tissues, forming combination organelles or mitochondria with lysosomal pockets. The two compartments of these dual bodies evidently have closely interrelated functions. The lamellae-containing mitochondria in alveolar cells may continue to function, as indicated by their topographical association with organelles involved in protein synthesis and plasmalemmal reorganisation. Acetyl coenzyme A, derived from membrane catabolism, may pass across the intercompartmental membrane barrier, a process facilitated by modification of the inner mitochondrial membrane, into the mitochondrion proper, where the acetate groups may enter the citric acid cycle.

Lamellated body contents typically undergo a normal exocytotic process. By contrast, OLB-derived lamellae invaginated by mitochondria may

have a different fate; they might not be eliminated into the alveolar cavity, but may remain within the organelles and serve to directly fuel mitochondrial function.

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New Zealand nemertines from kelp holdfasts: Heteronemertinea 1. *Adenorhagas aurantiafrons* gen. n., sp. n.

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Abstract A small heteronemertine with a brilliant orange cap at the tip of the head was found in kelp holdfasts at Kaikoura and Leigh, New Zealand. The species is characterised by presence of a large number of gland cells in the lateral cephalic fissures, extensive development of sensory cells posteriorly in the cephalic fissures, and the absence of an excretory system. The genus *Adenorhagas* is erected to contain this new species. It differs from *Micrura* in its absence of longitudinal muscles between the rhynchocoel and foregut, and the presence of two longitudinal muscle layers separated by a circular muscle layer with one muscle cross in the proboscis.

Keywords Nemertinea; *Adenorhagas aurantiafrons*; new genus; new species; systematics; taxonomy

INTRODUCTION

Some cryptic nemertineans aggregate under stones, but most are encountered as isolated individuals in restricted interstitial spaces such as among the byssal threads of pelecypod molluscs, coralline turf, algal mats, or crevices in rocks. Large numbers of individuals and species frequently occur in kelp holdfasts which may be the primary habitat niche for many of them. Holdfasts which washed up on the beaches at Kaikoura and Leigh, New Zealand between mid-February and Mid-April 1986 yielded only two species of Heteronemertinea. Most of the

specimens of both species were young and immature suggesting that the holdfasts were being utilised by them as a "nursery" rather than as a permanent habitat niche.

MATERIALS AND METHODS

Collection, preservation, and preparation of slides of serial sections were described in Riser (1988). In addition, some sections were stained with the copper chrome hematoxylin technique of Bensley & Bensley (1938) in order to follow nerve tracts.

SYSTEMATICS

Adenorhagas aurantiafrons n.g., sp.n.

Description.

EXTERNAL FEATURES. The largest specimen was female, 24 mm long by 1.1 mm diameter fully extended while gliding. Anterior and posterior ends of living individuals are bluntly rounded, and the body is round with a uniform diameter. Upon preservation, some specimens contracted so that the anterior quarter to a half formed an inflated, elongated cone. Several individuals fragmented, even though apparently well-anaesthetised. Basic body color of small individuals was chalky-white with a bright orange cap at the tip of the head. An orange stripe continued down the dorsum of most specimens > 10 mm long, and the entire dorsum of individuals > 18 mm long was a dirty orange colour except for the bright orange cap. A minute, papilla-like caudal cirrus is present. The lateral cephalic furrows are short, shallow, and difficult to see, reaching to the level of the minute pore-like mouth. Eyes are absent.

BODY WALL. The epidermis is of rather uniform thickness throughout the body. It is dominated by densely packed (Fig. 6, 7) goblet cells 26-32 µm tall containing an homogeneous, strongly azanophilous secretion. Cyanophilous (mucous) goblet cells are widely scattered in the epidermis

(surfacial sections indicate a ratio of about 1:100 azanophilous cells), and the necks of subepidermal glands are present. Gland cells are rare in the epidermis of the caudal cirrus (Fig. 5). The epidermis rests on a relatively thick basement membrane, at least half as thick as the subepidermal muscle layers, of which the circular layer is very thin. This muscle layer appears to give rise via radial fibres to the horizontal muscle bar between the anterior end of the cephalic blood lacuna and the bases of the apical sensory organs. The subepidermal longitudinal muscle layer is one to two bundles thick, depending upon contraction or expansion of the body wall. Each bundle contains three to six fibres and is surrounded by a thin membrane. The cell bodies of the subepidermal glands are packed together immediately beneath these bundles.

A small number of homoserous gland cells are present in the subepidermal gland layer, which is dominated by mucous and basophilic bacillary glands and not separated from the outer longitudinal muscle layer (OLM) by a connective tissue layer. Cell bodies of the mucous glands are packed against the OLM. The cell bodies of a few of the bacillary glands abut the OLM, but the majority occur in the outer half of the gland layer. Subepidermal mucous glands are absent around the mouth. Mucous glands dominate in the pre-cerebral region where two groupings occur, i.e., frontal glands, which are not abundant, and the more peripheral subepidermals, which discharge through the epidermis, especially near to but outside the cephalic furrows.

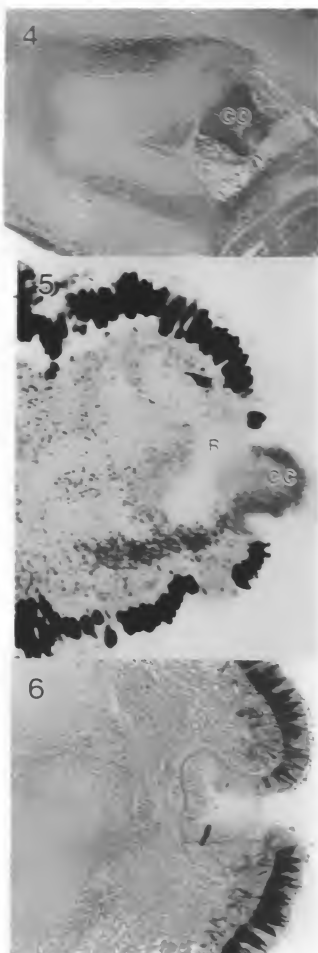
The postoral OLM is more than twice as thick as the inner circular muscle layer (ICM), and is separated from it by a thin layer of connective tissue which is thickest over the lateral nerve cords. The ICM extends as a ring from the posterior end of the body almost to the anterior end of the cephalic blood lacuna but is somewhat disorganised between that point and the horizontal muscle bar. It is thicker than the internal longitudinal layer (ILM). Both of these layers are disrupted at the mouth, at the proboscis diaphragm (by the passage of the OLM fibres into the proboscis), and at the entrance of the cerebral canals into the cerebral organs. The OLM and ILM do not unite at the mouth to pass around it as a composite muscle. The ILM splits around the

buccal cavity but does not extend ventrally beneath the esophageal nerves and as a result, is absent between the ICM ring and the ventral wall of the initial portion of the esophagus. The ventral arms of the ILM do not meet around the esophagus until shortly before the esophageal nerves become indistinct. A few fibres from the ICM become isolated beneath the esophageal epithelium but this situation does not occur posteriorly where the ILM forms a continuous layer. The ILM and rhynchocoel LM unite at the proboscideal sphincter and continue as a thin layer in the outer walls of the cephalic blood lacuna and beyond the lacuna to the anterior tip of the body. It is not strongly developed as a compact muscle in the wall of the lacuna. Radial muscle fibres are present throughout the body and pass through the subepidermal gland layer and OLM to insert in the ICM or through it to the tunica propria of the gut. Some ventro-lateral radial fibres branch to form isolated circular fibres beneath the epithelium of the esophagus ventrally. In the pre-cerebral region, radial fibres pass through the ICM and ILM, to form the rhynchodaeal/rhynchocoel circular muscle layer (Fig. 2) and divide the blood lacuna into three channels. Dorsoventral muscles are present in the intestinal region of the body between the caeca. No muscles are present between the esophagus and rhynchocoel, and with the exception of the previously mentioned branches of the radial fibres which produce short strands of circular fibres beneath the esophagus, there are no muscle layers associated with that portion of the foregut.

Parenchyme is present around the gonads but otherwise is evident only around the rhynchocoel.

PROBOSCIS APPARATUS. The ciliated proboscideal furrow extends almost to the apex of the head, but its characteristic epithelium continues forward to the tip as a band on the ventral surface. Goblet cells and the necks of subepidermal glands are absent from the epithelium of the band, furrow, and rhynchodaeum, and the rhynchodaeal cells are unciliated. The basement membrane is exceedingly thin so that the longitudinal muscle bundles accompanying the furrow seem almost to be in contact with the epithelium. A thick nerve plexus, which is broken dorsally and incomplete ventrally,

Fig. 1-6 *Adenorhagas aurantiafrons*. 1. Cross section through anterior region of rhynchodaeum. IL, internal longitudinal muscles; NP, neural plexus. 2. Cross section through rhynchodaeum immediately anterior to proboscis diaphragm. NP, neural plexus. 3. Cross section through cephalic fissure at posterior end of papilla of cerebral organ canal. CO, cerebral organ; G, cell bodies of sensory cells; LN, lateral nerve; SE, sensory epithelium. 4. Longitudinal section through brain. CO, cerebral organ. 5. Longitudinal section of caudal end. CC, caudal cirrus; R, rectum. 6. Cross section through anterior portion of cephalic fissure.



lies outside of these muscle bundles behind the rhynchodaeal pore. The dorsal expansion of the rhynchodaeum is in contact with the ventral wall of the cephalic blood lacuna. A small dorsolateral bundle of longitudinal fibres is trapped between the ventral wall of the lacuna and the rhynchodaeum on each side. The ventral expansion of the lacuna is blocked by bundles of longitudinal muscle fibres along the lateral walls of the rhynchodaeum (Fig. 2). These "rhynchodaeal" muscles are a thickened part of the ILM which is continued dorsally as a thin layer enclosing the outer wall of the lacuna. The two lateral bundles do not meet in the mid-ventral line. A few radial fibres pass through this point of communication to form a sparse rhynchodaeal circular muscle layer beneath the epithelium. Fibres from the inner side of the OLM bend medially at the proboscideal diaphragm immediately in front of the dorsal brain commissure and form the longitudinal muscle layers of the proboscis. These fibres enter primarily through the dorsal and ventral gaps in the nerve plexus around the rhynchodaeum, although a few fibres also pass through the lateral walls of the plexus. The two lateral proboscideal nerves enter ventro-laterally at the diaphragm, initially between the epithelium and the longitudinal muscles, but shortly come to lie within the longitudinal layer. As the neural plexus forms between the two proboscideal nerves, small blocks of longitudinal fibres, isolated between the nerves and the epithelium, expand to form the outer longitudinal muscle layer of the proboscis. Circular muscles adjoin the plexus forming a loop with fibres passing through the inner longitudinal muscles as a single muscle cross to encircle the proboscis as a layer one fibre thick, beneath the endothelium. The circular muscles adjacent to the plexus thicken and throughout the major portion of the proboscis appear to be bipartite, i.e., a layer of concentric fibres against the plexus separated by a thin layer of parenchymatous connective tissue from the fibres participating in the loop.

The epithelium of the proboscis initially consists of simple columnar cells. Slightly behind the initial muscle cross, the epithelium becomes glandular, but retains a uniform height. Cells producing the rhabditoids (nematocysts of Hubrecht 1887; acidophilic rods of Jennings & Gibson 1969; cytoplasmic masses of Iwata 1970; rhabdites of Gontcharoff 1957; Ling 1971; Gibson 1981) occur on the side opposite the muscle cross and thus the rhabditoid packets at first are present in only one side of the lumen (Fig. 9). The epithelial spines

(Fig. 10) appear at the same time. Their relationship to the cells on the rhabditoid side is unclear, but on the opposite side, they form a dense rake-like denticulated surface. The spines (Iwata 1967, 1970; Anadon 1971, 1976, referred to them as stylets, but this term, usually applied to a totally different enoplous proboscis organelle, is not applicable to the insoluble hollow thorn-like structures of the heteronemertine proboscis), vary in length up to 38 μm in length. Our TEM observations show that the "accessory rods" recorded by Ling (1971) enclosing the flagellum of his putative "sensory" cells are the walls of the spines. In the main body of the inverted proboscis, three or four longitudinal ridges covered with glandular cells are apparent in cross sections, but may be fixation artifacts resulting from contraction of the circular muscle fibres. Cells producing rhabditoids are uniformly distributed in the epithelium of the main body of the proboscis. The rhabditoids are neatly bundled into packets with the long axes directed toward the lumen of the proboscis. The distal surface of each packet is round, and the packets appear as rectangles when viewed from the side. Extruded rhabditoids range from less than 3 μm to almost 10 μm in length. In the main body of the proboscis, they are mostly in the 9–10 μm range in the large packets which dominate in this region.

The proboscis is attached to the wall of the rhynchocoel in the region of the first appearance of gonads.

The rhynchocoel extends to the posterior end of the body. Its walls are very thin and the two muscle layers do not intermingle. The weak development of the muscles and the absence of supporting tissue between the rhynchocoel and foregut allow for two artifacts in the esophageal region; if the proboscis is ejected, the rhynchocoel can inflate to occupy most of the diameter of the body, and if the proboscis is forced forward on fixation, the rhynchocoel usually takes on a figure-8 shape as if there were a ventral diverticulum. The circular muscle layer of the dorsal wall of the rhynchocoel is in intimate contact with the ILM in the foregut region of the body but there is no intermingling of fibres.

The wall of the rhynchocoel beneath the epithelium, initially consists of connective tissue. A short distance behind the diaphragm, a single row of longitudinal muscle fibres is present dorsally in the connective tissue. Near the ventral brain commissure, additional longitudinal fibres are present in the lateral walls. The ring of longitudinal fibres is completed behind the origin of the

rhynchocoelic villus. Transverse muscle fibres between the dorsal ganglia and lateral nerve cords pass between the rhynchocoelic epithelium and the ILM with branches (or extensions) spreading beneath the epithelium to augment the rhynchocoelic CM. Fibres from the ICM above the buccal cavity form a broad attachment to the rhynchocoel further enhancing the circular muscle layer.

ALIMENTARY CANAL. The small, pore-like mouth (Fig. 7, 8) opens on the ventral surface a short distance behind the brain. The epithelium of the mouth is non-glandular and the underlying basement membrane is not apparent at the light microscope level of observation. The oral epithelium extends inwards a short distance and meets the epithelium of the buccal cavity without intergradation. The epithelium of the buccal cavity and esophagus is dominated by acidophilic and basophilic gland cells, some of which expand beneath the epithelium but do not form a subepithelial gland layer. The epithelium of the buccal cavity contains a higher proportion of mucous cells than does that of the esophagus. Nuclei of the ciliated "support" cells lie near the distal ends of those cells. The division of the foregut into two regions is arbitrary and based upon the presence of the subepidermal circular muscles which allow for the eversion of the walls of the buccal cavity through the mouth. Sections show a slight admixture of foregut and intestinal cells at the juncture of those two regions. The intestine almost immediately expands laterally to form the first pair of diverticulations. Very few of the intestinal cells beneath the dorsal blood vessel contain digestive granules.

BLOOD VASCULAR SYSTEM. The dorsal and two ventro-lateral (intestinal) blood vessels anastomose in a sinusoidal mesh around the posterior end of the intestine. Toward the anterior end of the intestine, a connective tissue wall is distinctly visible around the dorsal vessel; however, the dorsal CT disappears near the juncture of the intestine and foregut and the endothelium bulges into the rhynchocoel as the rhynchocoelic villus. The two intestinal vessels dissolve in the same region producing a sinusoidal mesh around the foregut. This mesh becomes dorsal around the buccal cavity expanding to form two lacunae near the anterior end of the cavity to either side of the rhynchocoel. Connective tissue and dorso-ventral muscles to the rhynchocoel separate the two lacunae ventrally, and strands of connective tissue passing between the fibres of the dorsal band of ILM to the wall of the rhynchocoel attach these

two together and restrict communication between the lateral lacunae. Transverse muscle fibres passing between the lateral nerve cords and the cerebral organs divide the lacunae into four chambers. The dorsal blood vessel exits the rhynchocoel and the ventral suspensor of the rhynchocoel ceases to continue forward, and thus, a single lacuna exists ventrally. The cerebral organs fill the lateral lacunae which meet over the rhynchocoel forming a single horseshoe-shaped space. Near the ventral cerebral commissure, the lacunae unite to form a ring around the rhynchocoel. The lacuna is broken up into a number of small spaces at the proboscideal diaphragm. The vascular tissue forms an arch around the rhynchodaeum which is attached to the adjacent tissues ventrally. A distinct lumen was not apparent in this portion of the vascular system of any of the specimens which were examined; however, the cavity was present in the prerhynchodeal lacuna at the anterior end of the system. (The sinusoidal appearance of parts of the vascular system may be an artifact resulting from the collapse of lacunar walls; however, in the genus *Micrura*, comparable parts of the system have a similar appearance.)

EXCRETORY SYSTEM. Excretory tubules are absent, and no organelles which could be interpreted as excretory in function could be found.

NERVOUS SYSTEM. The pre-rhynchodaeal tissue contains much material which stains as if of a neural nature but distinct nerve tracts are not evident. The neural tissue condenses around the rhynchodaeum as a plexus of anastomosing longitudinal tracts (Fig. 1). The two sides of the plexus are of equal thickness (Fig. 2), but dorsally and ventrally only occasional strands are present.

The dorsal and ventral cerebral lobes are united anteriorly, and the lobes of each side are connected by commissures; the ventral commissure is about three times as thick as the dorsal. The longitudinal tracts from the rhynchodaeal/rhynchocoel plexus extend along the medial sides of the cerebral ring, the majority eventually disappear in a dorso-medial lobe of the ventral ganglion. A thin connective tissue sheath encloses the cerebral neuropil and demarcates the lobes of the ganglia. A proboscideal nerve arises from the anterior end of each ventral ganglion. The dorsal ganglia are bifurcated posteriorly (Fig. 4). A thin commissure links the two lateral nerve cords anterior to the buccal cavity and gives rise to two esophageal nerves which extend around the buccal cavity and ventro-laterally beneath the anterior one-fifth of the esophagus.

The lateral nerve cords are united by a continuous plexus in the connective tissue between the CM and ILM behind the mouth. A dorsal nerve is not evident in the plexus. Neurochord cells are absent.

SENSORY SYSTEM. A small quadripartite group of frontal gland cells discharge amongst the three apical sensory organs. The frontal glands arise slightly anterior to the rhynchodaeal pore but far enough in front to not be confused with the anterior end of the cephalic blood lacuna.

The epithelium of the cephalic fissures is densely ciliated and sharply demarcated (Fig. 6) from the epithelium of the body surface. It contains mucous and pale azanophilous flask cells, and the necks of a few small basophilic subepidermal gland cells which are not arranged in packets. The basement membrane beneath the floor of the fissure is thick. Sensory cells in the epithelium were not evident anterior to the brain. The opening of the cerebral organs is at the tip of a glandular papilla toward the posterior end of each fissure and the fissures are flask shaped posteriorly, i.e., with a broad floor. The epithelium of the papilla consists primarily of large azanophilous flask cells and a few mucous flask cells (Fig. 3), both similar to those of the body epidermis. The epithelium of the floor around the papilla consists almost entirely of sensory cells, the nuclei of which form a compact ring beneath the epithelial layer (Fig. 3).

The cerebral organs are massive. The canal enters through the papilla and the epithelium is dominated by sensory cells. The canal turns posteriad and then ventrad. The secretory glands occur dorsally and ventrally and are not divided into anterior or posterior fields. They discharge into the canal near the initial flexure. The cell bodies of the vesicular glands are associated with the terminus of the canal and occupy the entire posterior end of each organ (Fig. 9). The cerebral organ nerve branches at the initial flexure of the canal, one branch passing into the ventral neuronal mass and one into the dorsal mass, while a main branch accompanies the canal almost to its posterior end. The dorsal and ventral branches subdivide to ramify through the neuronal masses. The cerebral organs are encased in a well-developed connective tissue tunic. The organs are fused with the large ventral

lobe of the dorsal ganglia. The dorsal lobe (Fig. 4) forms a hood over the anterior ends of the organs separated from them by the connective tissue sheath. The organs project into the cephalic blood lacuna which, in the absence of a dorsal septum, are not restricted symmetrically to one side or the other.

REPRODUCTIVE ORGANS. Two of the specimens contained gonads. Both were female and the oocytes were not undergoing vitellogenesis nor were any evidences of ducts present. The number of oocytes developing in each gonad was small.

Type data. Holotype. AMNH 307 serial cross section, 12 slides. Paratype. AMNH 308, serial longitudinal section, 2 slides; USNM 131997, serial cross section, 13 slides

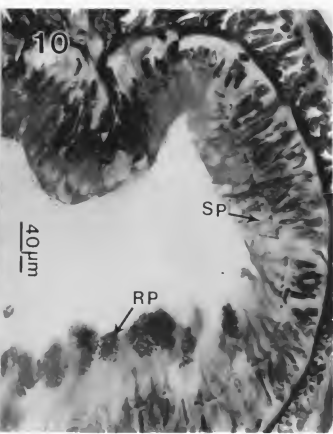
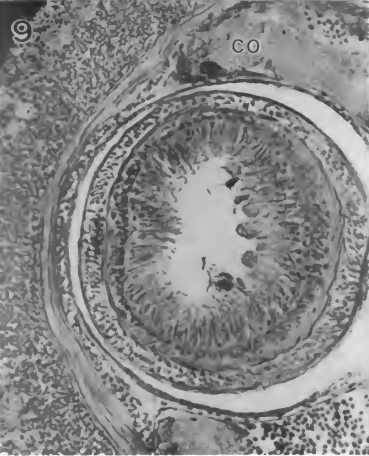
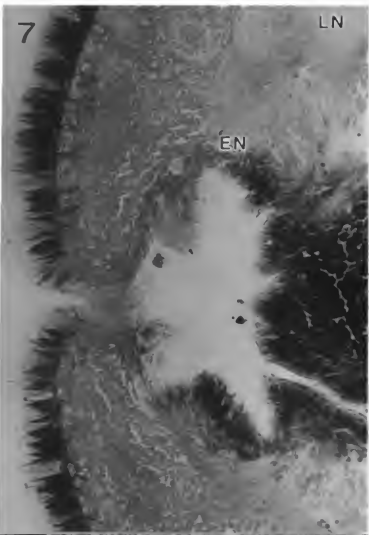
Other material. Seventeen living specimens from type locale and source; one specimen from holdfast of *Ecklonia radiata* washed up on Goat Island Beach, Leigh, N.Z., March 1986. Longitudinal serial sections of one specimen and serial transverse sections of seven others were utilised in this study.

Etymology. Gr.; adeno, gland; rhagas, fissure.

Type locality. Kaikoura, New Zealand, from holdfast of *Lessonia variegata*, 6 March 1986.

Remarks. Gibson (1981) produced a table based upon the morphological characters which Friedrich (1960) had advocated for generic diagnosis in the Heteronemertinea. In 1985, Gibson furnished a table, with additional characters in which he distinguished groups based upon the arrangement of the muscles layers in the proboscis. This table pointed out critical problems not only in generic diagnoses, but also in any efforts in phylogenetic systematics. Most heteronemertine species have been placed in the genera *Cerebratulus*, *Lineus*, and *Micrura*. The majority of the descriptions of species assigned to these genera are incomplete or inadequate, and as Table 2 of Gibson (1985) clearly shows, these genera are not self-contained groups of species, e.g., autapomorphies are not evident. Phylogenetic relationships within each of the groups of genera remains to be analysed. Taxonomists have long recognised that a genus is what the authority determines it to be, and, in establishing a phylogenetic system, supraspecific taxa are

Fig. 7-10 *Adenorhagas aurantiafrons*. 7. Cross section through mouth. EN, esophageal nerve; LN, lateral nerve. 8. Longitudinal section through mouth. 9. Cross section through anterior region of inverted proboscis. CO, cerebral organ. 10. Cross section of inverted proboscis. RP, rhabditoid packet; SP, proboscideal spine.



"arbitrary labels" (Ax 1987: 237). The proliferation of monotypic genera diagnoses in the Heteronemertinea as the result of more complete descriptions will facilitate rather than handicap phylogenetic analyses.

The occurrence of secretory cells in the epithelium of the cephalic fissures of *Adenorhagas aurantiafrons* to which the generic name refers, is unusual but not restricted to the genus. They increase in abundance posteriorly until the sensory cells become dominant in the epithelium.

There is no separation into OLM and subepidermal LM in the absence of subepidermal glands around the mouth. Among heteronemertines, compression of the oral epithelium between the epithelium of the buccal cavity and body epidermis as the result of contraction, usually inhibits observation of this feature. Densely arranged glands are responsible for the arbitrary (but useful in descriptions) division of what really is one muscle layer into two. Stiasny-Wijnhoff (1942) referred to the subepidermal glands of *Micrurina* occurring between the bands of OLM which extended between the subepidermal CM and the ICM. She stated that a subepithelial LM was absent. In areas where the subepidermal glands of *Lineus bicolor* Verrill, 1892 are packed together, I have observed that longitudinal muscle bundles of about equal size occur either subepidermally or between the bases of the glands and the ICM, and where the glands are less numerous (or densely packed) a single layer (one bundle thick) occupies this space. An examination of lineid heteronemertines at my disposal indicates that the ILM also blends into the longitudinal muscle organisation around the mouth, except in those species in which the subepidermal buccal glands press against (*Cerebratulus bicornis*, Joubin & Francois, 1892) or pass through (*Micrura alaskensis*, Coe, 1901) the ICM below the buccal nerves. In *Adenorhagas aurantiafrons* the ILM is blocked by the esophageal nerves from combining with the other longitudinal muscles. The combination of subepidermal LM, ILM, and OLM around the mouth is distinct in *Micrura fasciolata*, Ehrenberg, 1831 (= *M. affinis* Gerard, Stimpson, 1853) from Massachusetts Bay. This may account for the diagram by Cantell (1975, fig. 1A) who worked with this species, being more accurate than that of Stiasny-Wijnhoff (1923, fig. 6) which unfortunately has been accepted as portraying the actual relationships of heteronemertine muscles.

Contraction of the precerebral region of heteronemertines during fixation results in a button-

hooking of the longitudinal muscles at the proboscis diaphragm. In well-anesthetised specimens, the common origin of the rhynchocoelic and internal longitudinal muscles is clearly apparent, as is the origin of the proboscideal longitudinal muscles from the outer longitudinal layer of the body wall in common with all other nemertines.

The small papilliform caudal cirrus of *A. aurantiafrons* is not readily seen on preserved specimens. It is a distinct postanal structure (Fig. 5) but could easily be overlooked. It is possible that other heteronemertine species also have papilliform caudal cirri that have not been recorded.

Dewoletzky (1887) concluded that certain nuclei beneath the epithelium of the cephalic fissures belonged to ganglion cells and that their connection with the modified epithelium of the walls and bottom of the fissures indicated a sensory function. Modern techniques have allowed us to determine that these "gangliengerne" are the subepithelial nuclei of sensory cells which extend into the epithelium. The sensory nature of the epithelium is frequently mentioned in descriptions of species, but the distribution of the sensory cells is neglected. In some species they occur in the walls as well as the floor, and in some throughout the entire length of the fissures. The apparent concentration of the sensory cells to the limited area around the papilla in *Adenorhagas* is unusual.

The morphology of *Micrura fasciolata*, the type species of the genus, was described by Friedrich (1960) and later with additions and illustrations by Cantell (1975). Friedrich (p. 53) noted the absence of a connective tissue layer in the cutis, that only two muscle layers with one muscle cross were present in the proboscis, and that the presence of longitudinal muscles between the rhynchocoel and foregut could not be ascertained. Cantell (fig. 2E) showed two layers and two muscle crosses, and referred to extensive development of CT in the cutis. He also noted the presence of longitudinal muscles between the foregut and rhynchocoel and correctly showed their derivation from the subepidermal LM in his diagram (fig. 1A). In 1976, Cantell (p. 120) stated that "a thick connective tissue layer in the interior cutis" was absent in all of the heteronemertines, including *M. fasciolata*, which he had described in 1975. His earlier references to a "cutis rich in connective tissue" was concerned with CT enclosing the subepidermal glands and did not refer to a CT layer.

Cantell (1976) verified the presence of two muscle layers and two muscle crosses in the

proboscis of *Lineus longissimus* (Gunnerus, 1770) as figured by McIntosh (1873/74, Pl. XXI, fig. 5). Thus, the type species of the genera *Lineus* and *Micrura* are in group B (Lineidae) of Gibson (1985). *Adenorhagas* with inner and outer longitudinal muscle layers separated by a circular, belongs to Group A (Cerebratulidae) according to the scheme suggested by Gibson (1985). The flask-shaped posterior portion of the cephalic fissures, with a glandular papilla bearing the opening of the cerebral organ canal, the absence of a CT layer beneath the subepidermal glands, as well as the absence of a complete connective tissue sheath enclosing the ganglion layer of the brain, and the presence of a caudal cirrus, would induce most workers to place the species in the genus *Micrura* if the proboscis was not retained. Historically, heteronemertine species missing a proboscis, have been described and named, or have been assigned to a genus, e.g., *Cerebratulides* Stiasny-Wijnhoff, 1942. This has not only produced many names of species which cannot be identified, but also disrupts efforts to clarify genera. Punnett & Cooper (1909) placed all heteronemertines with a subepidermal connective tissue layer in the genus *Lineus* (a valid character), and all without this layer in *Cerebratulus* (also valid). In the Appendix to their paper they referred to the genus *Micrura* as a valid entity, but, based on the single character used in their paper, all valid species of *Micrura* would have had to be placed in *Cerebratulus*. Thus, while they simplified their own work, they created havoc with heteronemertine systematics and the *Lineus* and *Cerebratulus* species which they described will probably all have to be considered *nomina dubia*. *Adenorhagas* probably is related to those species described in the genus *Micrura* which have three muscle layers in the proboscis, one muscle cross, lack longitudinal muscles between the rhynchocoel and foregut, and lack a CT layer between the subepidermal glands and the OLM. These species must be removed from the genus and reassigned.

According to the characters listed by Gibson (1985), *Adenorhagas* is most similar to *Micrurina* among the 13 genera remaining in group A, following the transfer of *Lineus* and *Micrura* to group B. Stiasny-Wijnhoff (1942) described *Micrurina* from an incomplete specimen which left unresolved the presence or absence of a caudal cirrus. *Micrurina* lacks apical sensory organs. Its rhynchodaeum is attached dorsally as well as ventrally, separating the cephalic blood lacuna into two spacious lateral lacunae. Lateral blood vessels

are present in the intestinal region and an excretory system is present. Also, there is no distinction between subepidermal longitudinal muscles and the OLM; the subepidermal glands pass inwards between the longitudinal bundles.

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The New Zealand species of the subfamily Metopiinae (Hymenoptera: Ichneumonidae)

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Abstract The New Zealand species of the ichneumonid subfamily Metopiinae are revised. Three new species are described, *Hypsicera nelsonensis*, *Sciron glaber*, and *S. enolae*. One cosmopolitan species, *Hypsicera femoralis* Geoffroy is recorded from New Zealand. *Carria nigripes* (Cameron) is synonymised with *C. fortipes* (Cameron). A key to species is included.

Keywords systematics; taxonomy; revision; key; parasitic Hymenoptera; Ichneumonidae; Metopiinae; new species; *Hypsicera*; *Carria*; *Sciron*

INTRODUCTION

The Metopiinae is a world-wide ichneumonid subfamily of about 540 valid described species (Fitton 1984). It is poorly represented in New Zealand, three species in two genera having been recognised previously (Valentine & Walker in press). Five species representing three genera are recognised in the present study, compared to 60 species in 9 genera in Britain (Gauld & Bolton 1988), 151 species in 21 genera in North America (Krombein et al. 1979), and 43 species, most undescribed, in 10 genera in Australia (Fitton 1984). Metopiinae are koinobiont endoparasitoids of Lepidoptera, ovipositing in the host larva and constructing a flimsy cocoon within the host pupa before emerging as adults (Gupta 1987). Diagnostic characters and a key to ichneumonid subfamilies are given in Gauld (1984). The generic diagnosis

for *Hypsicera* Latreille is based on the two species described and the generic diagnosis for *Sciron* Fitton is based on the Australian and New Zealand species.

Conventions

Area codes quoted for specimens follow Crosby et al. (1976). The following collection abbreviations are used: LCNZ: Lincoln University, PO Box 84, Canterbury, New Zealand. NZAC: New Zealand Arthropod Collection, DSIR Plant Protection, Private Bag, Auckland, New Zealand. OMNZ: Otago Museum, Great King St., Dunedin, New Zealand. BMNH: Museum of Natural History, Cromwell Rd., London SW7 5BD, England.

Morphology

Morphological terms follow Gauld (1984). The terms OD and OOL refer respectively to the diameter of the posterior ocellus at its widest point and the ocular-ocellar line, i.e., the shortest distance from the eye to the posterior ocellus. Gaster, as used here, refers to that portion of the abdomen posterior to the propodeum. Tergite 1 (T1) refers to the first gastral tergite, i.e., the second abdominal tergite. F1 of the antenna refers to the first flagellar segment, i.e., the third antennal segment.

KEY TO GENERA AND SPECIES OF NEW ZEALAND METOPIINAE

1. Anterior transverse carina of propodeum present (Fig. 1) or absent only medially *Hypsicera* 3
- Anterior transverse carina of propodeum completely absent (Fig. 2, 3) 2
2. T1 of gaster approximately as long as its greatest width (Fig. 4, 5). Occipital carina entirely absent *Carria fortipes* (Cameron)
- T1 of gaster approximately 2X as long as its greatest width (Fig. 7, 9). Occipital carina present dorsally at least *Sciron* 4

3. Larger species, forewing length 4.1–5.1 mm. F1 of antenna 2× length of F2. Anterior transverse carina of propodeum absent medially, propodeal spiracle elliptical (approx. 1.5× as long as wide) *Hypsicera femoralis* Geoffroy
- Smaller species, forewing length 2.8–3.4 mm. F1 of antenna no more than 1.5× length of F2. Anterior transverse carina of propodeum present medially, though weak, propodeal spiracle circular *Hypsicera nelsonensis* n. sp.
4. OD greater than or equal to OOL. Malar space less than basal mandibular width. Notauli inconspicuous. Propodeum glabrous, all carinae effaced except for faint traces of median longitudinal carinae (Fig. 6). Hind tibiae dark brown basally and whitish-yellow apically. T1 of gaster with sides sub-basally concave in dorsal view *Sciron glaber* n. sp.
- OD approximately 0.6× OOL. Malar space greater than basal mandibular width. Notauli distinct for 0.5× length of mesoscutum. Propodeum slightly rugose with median longitudinal carinae clearly visible (Fig. 8). Hind tibiae dark brown. T1 of gaster sub-basally parallel sided in dorsal view (males only) *Sciron enolae* n. sp.

Genus *Hypsicera*

Hypsicera Latreille, 1829: 288

Type species. *Ichneumon femoralis* Geoffroy (by monotypy).

A large genus with an Australasian, Ethiopian, Oriental, and Holarctic distribution.

Description. Small to medium-sized ichneumonids, forewing length 2.8–5.1 mm.

Head: Black, antennae yellowish brown to dark brown/black. Face in lateral view produced to blunt point forming shelf below antennal sockets. In frontal view upper edge of shelf produced between sockets in short curve and extended as carina from outer edge of antennal socket to eye. Face punctate to finely rugose, punctations less dense toward clypeus. Clypeus slightly indented medially. Mandible bidentate or with one tooth and truncation. Malar space greater than basal mandibular width. Vertex finely punctate, back of head dropping at right angles from hind margin of posterior ocelli. Occipital carina present dorsally or absent.

Thorax: Black, mesoscutum closely punctate, covered in short yellowish-white pubescence.

Notauli indicated anteriorly only. Scutellum flat to very slightly convex in lateral view, finely punctate. Mesopleuron finely punctate and hairy anteriorly, smooth and shining posteriorly. Epinemial carina complete, running to subtegular ridge. Metapleuron smooth and shining. Propodeal carination complete except medial portion of anterior transverse carina may not be present. Propodeum abruptly declivous at apical transverse carina. Spiracle circular to elliptical.

Forewing with 3r-m absent, 2r-m equal to or longer than abscissa of M between 2r-m and 2m-cu. Hindwing with distal abscissa of Cu1 present but faint or absent, Cu1+cu-a angled below midpoint.

Legs from reddish brown to brownish yellow, tarsal claws simple or pectinate.

Gaster: Black, grading to dark reddish brown posteriorly. T1 narrow basally, broad apically with two lateromedian longitudinal carinae extending approximately half length of tergite. Spiracle from 0.3 to 0.4 distance along tergite from base. T1 as long as or longer than broad, all other gastral tergites broader than long. Laterotergites vestigial on T1, small on T2, and wide on T3–T7; separated by defined crease only on T2–T4. Ovipositor not extended beyond apex of gaster.

Hypsicera femoralis (Geoffroy)

Ichneumon femoralis Geoffroy, 1785: 395.

Description. Medium-sized ichneumonids, forewing length 4.1–5.1 mm.

Head: Antennae dark brownish-yellow, F1 2× length of F2. Upper edge of facial shelf produced into a short blunt curve between antennae. Face closely and finely punctate, almost rugose, excepting only a small shining patch above clypeal margin. Anterior tentorial pits conspicuous. Mandibles slightly tapered, bidentate, with lower tooth slightly smaller and shorter than upper. Occipital carina distinct laterally, obsolete ventrally.

Thorax: Propodeal carination complete except median portion of anterior transverse carina absent. Spiracle elliptical, approximately 1.5× as long as wide.

Forewing with 2r-m slightly longer than the abscissa of M between 2r-m and 2m-cu. Hindwing with distal abscissa of Cu1 present but faint.

Legs and all coxae dark reddish yellow, all tarsal claws sparsely pectinate.

Gaster: T1 with spiracle situated 0.4 distance along tergite from base on lateral longitudinal carina. All tergites smooth and shiny, very finely punctate.

Material examined. Four specimens, NZAC.

Distribution. Europe, North America, Africa, Asia, Japan, Taiwan, Japan, Hawaii, New Zealand: AK.

Host Records. Townes (1947) notes that *H. femoralis* is a parasite of clothes moths, usually collected in buildings.

Remarks. The earliest record of *H. femoralis* in NZ is 1977. Only four specimens have been collected, all from Auckland and all from inside houses.

Hysicera nelsonensis, new species

Description. Small ichneumonids, forewing length 2.8–3.4 mm.

Head: Antennae yellowish-brown basally, dark brown apically, F1 no more than 1.5× length of F2. Upper edge of facial shelf produced to a sharp curve between antennae. Face finely punctate, punctures close near antennal sockets and sparse approaching clypeal margin. Clypeus smooth directly above clypeal margin, delimited by a semicircle of slightly larger punctures. Anterior tentorial pits inconspicuous. Mandibles punctate, tapered, with one large tooth and a truncation. Occipital carina absent.

Thorax: Propodeum with carination complete, although median portion of anterior transverse carina may be weak (Fig. 1). Propodeal spiracle circular.

Forewing with 2r-m approximately the same length as the abscissa of M between 2r-m and 2m-cu. Hindwing with distal abscissa of Cu1 absent.

Legs testaceous, coxae 2 and 3 darker, fore tarsal claws sparsely pectinate, mid- and hind tarsal claws simple.

Gaster: T1 with spiracle situated 0.3 distance along tergite from base on lateral longitudinal carinae.

Type data. **Holotype.** Female, New Zealand NN, 10 Jan 1928, E. S. Gourlay (NZAC). **Paratypes** (19 females, 0 males). NN- 13 females, Nelson, 19 Jan 1924, 10 Mar 1926, 10 Mar 1926, 16 Mar 1927, 10 Jan 1928, 21 Jan 1928, 21 Jan 1928, 9 Feb 1928, 14 Feb 1928, 16 Feb 1928, 20 Feb 1928, 28 Dec 1938, 4 Mar 1949, E. S. Gourlay; 1 female, Nelson, 1938, ex *Carposina adreptella*, 95/51; 1 female, Nelson, Dun Mt, 30 Apr 1934, D. Wright; 1 female, Nelson, 15 Nov 1954, AWP, in house; 1 female, Nelson, 8 Mar 1966, B. B. Given. SD- 1 female, D'Urville I, Kapowai, Apr 1971, F. Alack, Litter 71/101. MC- 1 female, Christchurch, 15.11.22. E. S. Gourlay.

Material examined. 20 specimens, NZAC.

Distribution. New Zealand: NN, SD, MC.

Host records. *Heterocrossa rubophaga* Dugdale (= *Carposina adreptella* of authors) (Lepidoptera: Carposinidae).

Remarks. Misidentified as *Hysicera femoralis* by Parrott.

Genus *Carria*

Carria Schmiedeknecht, 1924: 112.

Type species. *Carria paradoxa* Schmiedeknecht (by monotypy).

A small Holarctic and Australasian genus.

Carria fortipes (Cameron)

Chorinaeus? fortipes Cameron, 1898: 29.

Chorinacus(!) forticeps(!) Cameron, 1903: 293

Chorinaeus nigripes Cameron, 1898: 30. New synonymy.

Chorinacus(!) nigripes Cameron, 1903: 293

Description. Medium-sized ichneumonids, forewing length 3.1–5.8 mm.

Head: Antennae dark brown to black, F1 longest flagellar segment. Face rugose, produced to a blunt point under antennal scrobes. Clypeal margin slightly concave medially. Mandible bidentate, upper tooth sharp, lower tooth blunt and shorter than upper. Malar space less than basal mandibular width. OD less than or equal to OOL. Occiput finely punctate, occipital carina completely absent. **Thorax:** Notauli inconspicuous, indicated only at anterior of mesoscutum. Mesoscutum finely punctate. Scutellum flat, less finely punctate than mesoscutum. Epicnemial carina complete, running to subtegular ridge. Propodeal carination ranging from two strong, complete lateromedian longitudinal carinae to these almost entirely effaced (Fig. 2, 3). Lateral parts of propodeum coarsely punctate, median area less punctate, may be rugose or smooth and shining. Posterior area usually smooth and shining. Spiracle subcircular. Metapleuron smooth and polished.

Forewing with areolet complete (1 specimen of 218 had 3r-m missing), 2m-cu joining distally to centre. Hindwing with Cu1+cu-a curved, rarely angulate.

Gaster: T1 short and broad, only slightly longer than greatest apical width (Fig. 4, 5) spiracle approximately 0.2 distance from base of tergite. T1 with or without two lateromedian longitudinal carinae extending up to two-thirds length of tergite (Fig. 4, 5). All gastral tergites closely punctate.

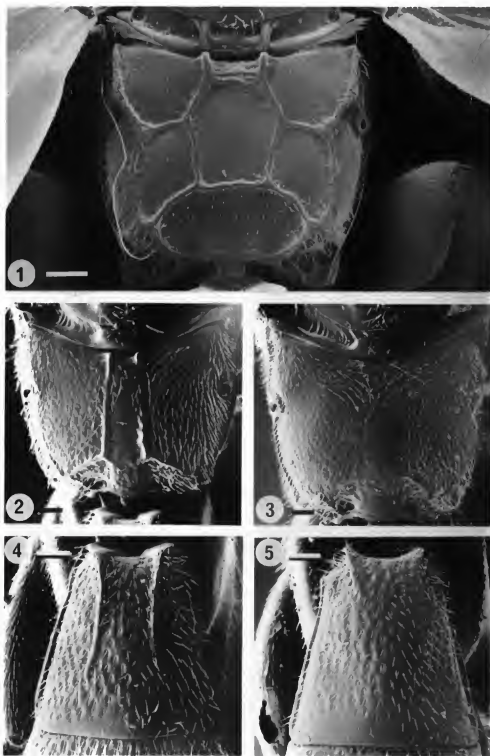


Fig. 1–(5) (1) Propodeum, *Hysiciera nelsonensis*, (2) Propodeum, *Carria fortipes* male, (3) Propodeum, *Carria fortipes* female, (4) Tergite 1 (T1) of gaster, *Carria fortipes* female, (5) T1 of gaster, *Carria fortipes* female. Scale bar = 0.1 mm.

Laterotergites of T1 narrow, those of T2–T4 increasing in width, that of T4 defined by a crease along entire length of tergite.

Female: Ovipositor without dorsal subapical notch, not or scarcely extending beyond apex of gaster.

Type data. New Zealand, Greymouth. (BMNH). Headless, and lacking one forewing.

Note. Cameron (1898) and Townes et al. (1961) have both recorded the holotype, wrongly, as a female. It is a male.

Material examined. 190 specimens, NZAC; 14 specimens, LCNZ; 14 specimens, OMNZ.

Distribution. ND, AK, BP, HB, TO, WI, WN/NN, SD, BR, KA, NC, MC, SC, WD, OL, FD, DN, CO, SL, SI.

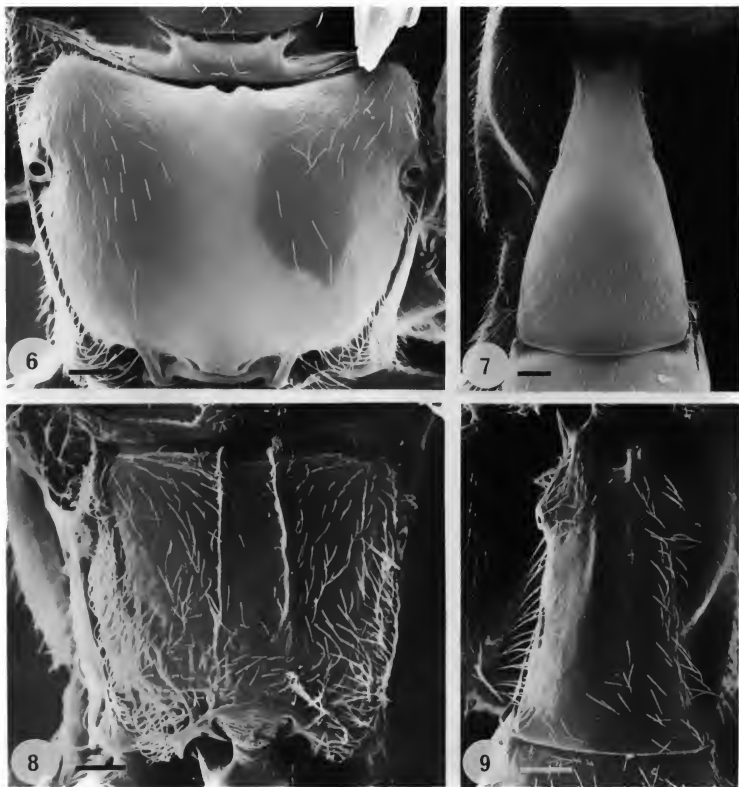


Fig. 6–9. (6) Propodeum, *Sciron glaber*, (7) T1 of gaster, *Sciron glaber*, (8) Propodeum, *Sciron enolae*, (9) T1 of gaster, *Sciron enolae*. Scale bar = 0.1 mm.

Host records. ?*Ctenopseustis* sp. (Lepidoptera: Tortricidae); *Pyrgotis plagiatana* Walker (Lepidoptera: Tortricidae); *Planotortrix excessana* Walker (Lepidoptera: Tortricidae); *Epalxiphora axenana* Meyrick (Lepidoptera: Tortricidae).

Remarks. Cameron (1898) described two species of *Carria* from New Zealand under *Chorinaeus*, *C. fortipes* and *C. nigripes*, commenting that *C. fortipes* differed from *C. nigripes* in “the petiole having two strong keels down its centre, which is, further, much

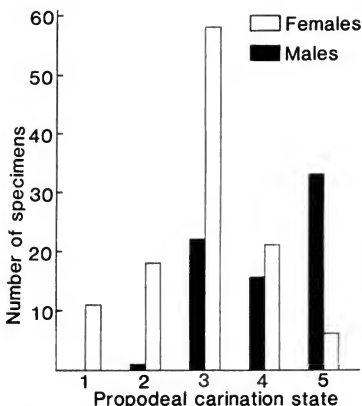


Fig. 10 Propodeal carination state (1–5) vs number of specimens for male and female *Carria fortipes*.

more distinctly raised and separated from the sides". He also noted that the lateromedian longitudinal carinae of the propodeum were much stronger in *C. fortipes* than in *C. nigripes*. In the 218 specimens of the genus examined in this study, the propodeal carination was found to range from almost entirely effaced, with only posterior vestiges of the lateral longitudinal carinae and a glabrous central area, to the condition described by Cameron as having two strong keels down the centre, i.e., the lateromedian longitudinal carinae present and complete. The longitudinal carinae on T1 (= petiole) were found to range from almost entirely absent, i.e., with only vestiges at the base of T1 to strong and extending approximately two-thirds length of the tergite. Carination of the propodeum was scored 1–5 (1= weakest state, carinae extending less than one-quarter length of propodeum; 5= strongest state, carinae extending entire length of propodeum and intermediate assigned values) and carination of T1 was scored 1–3 (1= weakest, 3= strongest). These values were plotted against numbers of specimens for each sex (Fig. 10, 11). If two species were present a bimodal distribution could be expected for each sex, i.e., a group of specimens representing Cameron's *nigripes* should have fallen into the lower range and a group representing *fortipes* into the higher range. However, for both characters, a peak

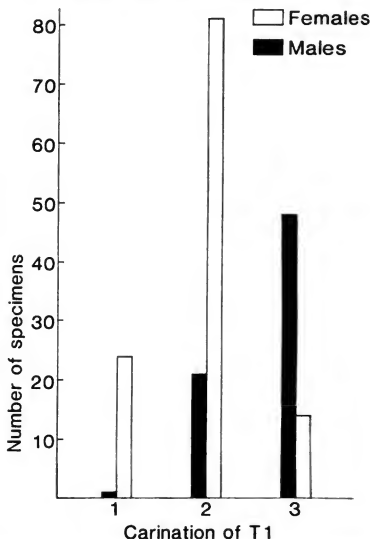


Fig. 11 Carination of T1 (1–3) vs number of specimens for male and female *Carria fortipes*.

of females resulted at the intermediate carination state and one of males at the strong state.

No other characters were found to vary consistently with propodeal carination or with carination of T1. Furthermore, series of specimens collected at the same time and in the same locality showed a range of these characters. I have concluded that the difference in these two characters represents a sexual dimorphism and not a specific difference and have accordingly synonymised *C. nigripes* with *C. fortipes*.

Cameron has mistakenly recorded the holotype of *C. fortipes* as a female; it is in fact a male and shows the stronger carination more typical of males of this species. Unfortunately, the holotype of his *C. nigripes* is missing but in all probability it would have been a female specimen, as he remarks on the weaker carination of the petiole and the median segment in his description.

Note. A single male specimen collected from Coronet Peak (OL) may represent a second *Carria*

species. It differs from *C. fortipes* in having the propodeal carination effaced and in having the occipital carina present but the shape of T1 is characteristic for the genus.

Genus *Sciron*

Sciron Fitton, 1984:361.

Type species. *Sciron fundator* Fitton (by monotypy).

A moderately large Australasian genus.

Description. Medium-sized ichneumonids, forewing length 3.5–5.9 mm.

Head: Antennae yellowish brown to dark brownish black. Combined face and clypeus curving gently to form a shallow shelf below antennal sockets. In frontal view upper edge of shelf produced in a blunt curve between antennae. Face finely transversely striate. Ocelli varying in size, OD ranging from 0.5 to 1.0× OOL. Occipital carina present dorsally and laterally, obsolete ventrally. Malar space from less than to greater than basal mandibular width. Clypeal margin from straight to slightly concave. Mandibles bidentate, upper tooth approximately 2× as long as lower; upper tooth sharply pointed, lower sharp or blunt.

Thorax: Notauli present anteriorly. Mesoscutum and scutellum finely punctate. Epicnemial carina complete, running to subtegular ridge. Propodeum with or without lateromedian longitudinal carinae, all other carinae absent. Metapleuron smooth and polished. Spiracle circular to slightly oval.

Forewing with 3r-m present and with 2r-m slightly shorter than the abscissa of M between 2r-m and 3m-cu. Arcolet rhombic with 2m-cu joining between centre and distal side. Cu-a subopposite M and Rs to distal to it by 0.5× its length. Hind wing with Cu1+cu-a with a distinct angulation well below centre and distal abscissa of Cu1 absent.

Gaster: Tergite 1 of gaster with or without lateromedian longitudinal carinae, approximately 2× as long as width at widest point. Spiracle from 0.2–0.4 distance along tergite from base.

Female: Ovipositor not or only slightly extending beyond end of gaster, with a large shallow dorsal subapical notch.

Sciron glaber, new species.

Description. Forewing length 4.3–5.9 mm.

Head: Ocelli large, OD greater than or equal to OOL. Malar space less than basal mandibular width. Mandible of female with blunt lower tooth, male

with sharply pointed lower tooth. Clypeal margin slightly concave.

Thorax: Notauli shallow, extending about one-third distance of scutum, scutellum closely punctate. Propodeum glabrous medially, slightly rugose towards lateral edges. All carinae effaced except for faint posterior traces of lateromedian longitudinal carinae (Fig. 6). Spiracle oval. Cu-a distal to M and Rs by 0.5× its own length.

Fore and mid legs yellowish-brown. Hind legs with coxae dark brown and yellowish-brown dorsally. Femur dark brown, tibiae dark brown basally and pale whitish-yellow apically. Tarsi yellowish-brown.

Gaster: Tergite 1 with sides sub-basally concave in dorsal view (Fig. 7) without lateromedian longitudinal carinae, spiracles approximately 0.3 distance along tergite from base. Laterotergites T1–T3 narrow, on T4 overlapping at posterior end of tergite, defined by a crease only anteriorly.

Type data. Holotype. Female: New Zealand NN, The Glen, 16 Mar 1951, A. W. Parrott 28/51 (NZAC). Paratypes (11 females, 2 males). AK- 1 male, Waitakere Ra, Jan 1981, J. S. Noyes; 1 female, Birkenhead, 21 Sep 1980, J. F. Longworth, Malaise trap in second growth bush; 1 female, Birkenhead, Nov 1980, J. F. Longworth, Malaise trap in second growth bush; 4 females, Birkenhead, Dec 1980, J. F. Longworth, Malaise trap in second growth bush; 3 females, Birkenhead, Jan 1981, J. F. Longworth, Malaise trap in second growth bush. BR- 2 females, 1 male, Lake Rotoiti, 600 m, Nov 1980, F. Dodge, Malaise trap, in edge of *Nothofagus* forest.

Material examined. 15 specimens, NZAC.

Distribution. New Zealand: AK, NN, BR.

Host Records. None.

Remarks. This species is distinguished from *S. enolae* and *S. fundator* Fitton by the glabrous propodeum with all carination effaced excepting faint posterior traces of the lateromedian longitudinal carinae.

Sciron enolae, new species.

Description. Forewing length 3.5–4.1 mm.

Head: Ocelli relatively small, OD approximately 0.6× OOL. Malar space greater than basal mandibular width. Mandibles bidentate, tapered from base. Upper tooth sharp, lower tooth sharp and about 0.5× length of upper. Clypeal margin straight or very slightly concave.

Thorax: Notauli deep and distinct for 0.5X length of mesoscutum. Scutellum relatively sparsely punctate. Propodeum with lateromedial longitudinal carinae present (Fig. 8). Lateral areas of propodeum slightly rugose, spiracle circular. Forewings with cu-a subopposite M and Rs, or distal by less than 0.5X length of cu-a. Forelegs dark brown except for yellowish region running length of ventral side of tibia.

Mid and hind legs dark.

Gaster: Tergite 1 with lateromedian longitudinal carinae extending 0.3–0.4 length of tergite. Spiracle 0.2–0.3 distance from base of tergite. Sides of T1 parallel basally in dorsal view (Fig. 9). Laterotergite of T4 defined by a crease at all but posterior end.

Female: Unknown.

Type data. **Holotype.** Male: New Zealand WN, Tararua Ra, Dundas Hut Ridge, 11 Feb 1985, C. F. Butcher, sweeping before Malaise trap (NZAC). **Paratypes.** WN- 1 male, Tararua Ra, Dundas Hut Ridge, 11 Feb 1985, C. F. Butcher, sweeping before Malaise trap. BR- 2 males, Porarari R, 35 m, 15 X 1984, J. W. Early, swept in forest; 1 male, Rahu Saddle, Rahu, Springs Junction, NZ, 31 X 1970, R. P. Pottinger. FD- 1 male, Mahere Basin, Tutoko Bench, Darran Mts, 1229–1524 m, 14 Jan 1977, J. S. Dugdale, sweeping.

Material examined. 3 specimens, NZAC; 3 specimens LCNZ.

Distribution. New Zealand: WN, BR, FD.

Host records. None.

Remarks. This species is distinguished from *S. nelsonensis* by the presence of lateromedial longitudinal carinae on the propodeum, and the deep notauli.

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Short communication

Storage of codling moth adults: effect on egg production

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Abstract The effect of storing unmated codling moth adults, *Cydia pomonella* L. (Lepidoptera: Olethreutidae) at 15°C for 0, 1, 2, 3, 4, 6, 8, and 10 days was investigated. There was no significant effect on egg production and egg mortality when adults < 12 h old were stored for up to 8 days. However, egg production was reduced by 50% after 10 days storage. The mean number of eggs laid per female per day declined on the fourth day after pairing, and was significantly lower on the fifth day for those adults stored 8 days. This study showed that adults could be stored and used without affecting their egg production and egg mortality.

Keywords Codling moth; *Cydia pomonella*; Lepidoptera; Olethreutidae; temperature; egg production; egg mortality; storage; quality assessment

INTRODUCTION

Although damage to many fruit crops by codling moth (*Cydia pomonella* L.) is minimised by pre-harvest insecticides, a mandatory postharvest disinfestation treatment of fruit exports using methyl bromide is often required by many importing countries to ensure that all life stages of this insect are killed. This disinfestation research has shown that the immature codling moth egg was the most resistant stage to this treatment (Yokoyama et al. 1988). In order to determine the specific treatment conditions required to kill the immature eggs, large

numbers must be produced from adults which often have to be collected and stored individually. The purpose of this study was to determine the effects of adult storage in the laboratory on the number of eggs produced per day, and egg mortality.

MATERIALS AND METHODS

The rearing procedures and protocols for the New Zealand codling moth strain were described by Ashby et al. (1985). Larval rearing was carried out at 25 ± 1°C, 50–60% RH, and a L:D of 18:6. Oviposition occurred under the same conditions except in total darkness.

Unmated adults < 12 h post eclosion were stored individually in 75 × 12 mm test tubes plugged with absorbent cotton soaked in a 10% honey solution at 15°C, 60–70% RH, and L:D 18:6 for 0, 1, 2, 3, 4, 6, 8, and 10 days. After the storage period, 20 pairs of adults per treatment were paired individually in perspex tubes for mating and oviposition. Eggs were laid on a scratched polythene sleeve inside the tube which was removed every 24 h, and stored at 15°C. The number of eggs laid per day and the egg mortality were recorded on each sleeve. A Student's *t* test was used to determine significant differences using MINITAB (Ryan et al. 1976).

RESULTS AND DISCUSSION

Adults that were not stored produced a median number of 161 eggs (Fig. 1), of which 97% were fertile. Storing adults for up to 8 days had no significant effect on egg production and mortality. However, egg production decreased ($P < 0.05$) after storage for 10 days with no significant difference in egg mortality.

In the control treatment, the adult females laid a minimum of 18 eggs per day per female from days 2–6 (Fig. 2). The mean number of eggs laid per female per day declined on the fourth day after pairing in control and in stored moths. The number of eggs was significantly lower on the fifth day for

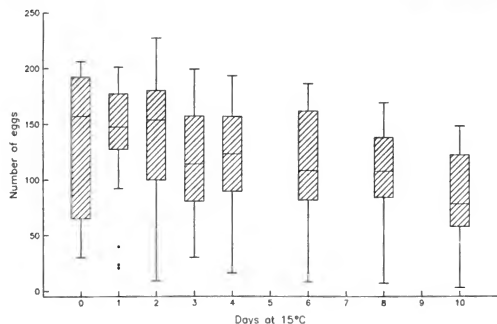


Fig. 1 Box plot summary of egg production when codling moth adults (<12h old) were held at 15°C. In the box plot the middle line represents the median, with the lines either side being the upper and lower 25% of the values either side of the median. The dotted lines above and below the boxes extend to incorporate 99% of the values in a normal distribution. Values that occur outside these limits are indicated by an *.

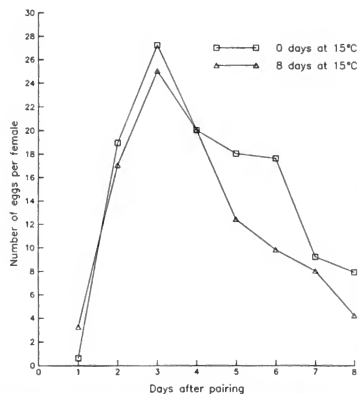


Fig. 2 Number of eggs laid per female per day at 25°C when adults (<12h old) were held at 15°C.

adults stored 8 days. As adults were used for disinfestation tests on days 3 and 4 after pairing, adults could be used after storage up to 8 days.

These results enabled us to formulate a standard procedure for the production of large numbers of eggs using standard mass-rearing procedures for codling moth (Ashby et al. 1985). Peak adult emergence from larval rearing trays occurred over

a period of 6 days, 27–32 days after infesting with neonate larvae. Newly emerged adults were collected daily over this period and stored at 15°C for 8 days or less. Adults were then pooled and paired in group mating cages (50 pairs/cage) at $25 \pm 1^\circ\text{C}$ for 2 days before being used for egg production in disinfestation research on days 3 and 4 after pairing.

The egg production of adults supplied for disinfestation research was monitored by comparing the number of eggs laid on pleated wax paper in group oviposition cages with those laid on different fruit cultivars. An average of 20, 22, 33, and 30 eggs per female per day were laid on wax paper, 'Granny Smith' apples, 'Red Delicious' apples, and on different cultivars of cherries respectively on days 3 and 4 after pairing. This confirmed that adults held up to 8 days retained optimum egg production on a variety of substrates.

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